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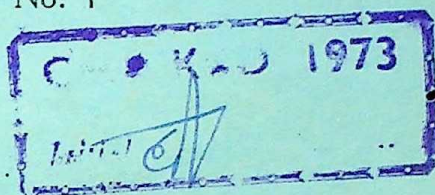
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JOURNAL
OF THE
ROYAL ASIATIC SOCIETY OF BENGAL
SCIENCE

Vol. IV, 1938, No. 1



CALCUTTA

PRINTED AT THE BAPTIST MISSION PRESS
PUBLISHED BY THE ROYAL ASIATIC SOCIETY OF BENGAL, 1, PARK STREET

Issued March, 1939

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JOURNAL
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SCIENCE

VOLUME IV

1938

The Histology and Physiology of the Intestine and
Hepato-pancreas of two Isopods, *Ligia exotica*
Roux, and *Armadillio elevatus* Verhoeff.

By MARY CHANDY.

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1. INTRODUCTION.

The histology of the digestive organs of Isopods has engaged the attention of several zoologists like Mayer (1879), Webber (1880), Huet (1885), Rosenstadt (1888), Ide (1892), McMurrich (1898), Murlin (1902), Apathy (1908), Jordan (1913), Nusbaum (1917-1920), Patrick (1927) and Nicholls (1931). They have made valuable contributions towards the elucidation of the problems of secretion, digestion, and absorption in the alimentary tract. But in the light of recent advances in cytology many points still remain to be elucidated, especially the secretory phenomena in the glandular cells of the hepato-pancreas. This aspect of the problem and the study of the cells in the living condition have been the chief interest in my work.

The specimens chosen for study were *Ligia exotica* Roux and *Armadillio elevatus* Verhoeff. The former is a common brackish water form of the Coovum River, Madras and is practically adapted for life on land, for it can live out of water for long hours. It is usually found crawling on the wet muddy banks of the river and its canals or clinging to the keels of boats. It is omnivorous in diet, and in the laboratory has been noted to eat even cork and sponge that were used as mere substrata for it to live on. *Armadillio* is a purely terrestrial form and lives under stones or decaying vegetable matter and feeds on organic debris.

2. THE ANATOMY OF THE DIGESTIVE ORGANS.

In both *Ligia* and *Armadillio* the alimentary canal is a straight tube, running through the middle of the body-cavity. The mouth is ventral in position and opens into the narrow oesophagus which dilates to form the so-called 'stomach' or the main part of the fore-gut. The fore-gut passes imperceptibly into the intestine. At the junction of the fore-gut and the intestine, in the mid-ventral line, opens the common median duct of the moniliform hepato-pancreatic glands of which there are three pairs in *Ligia* and two in *Armadillio* extending the whole length of the body-cavity and practically enveloping the intestine (fig. 1, a. and b.).

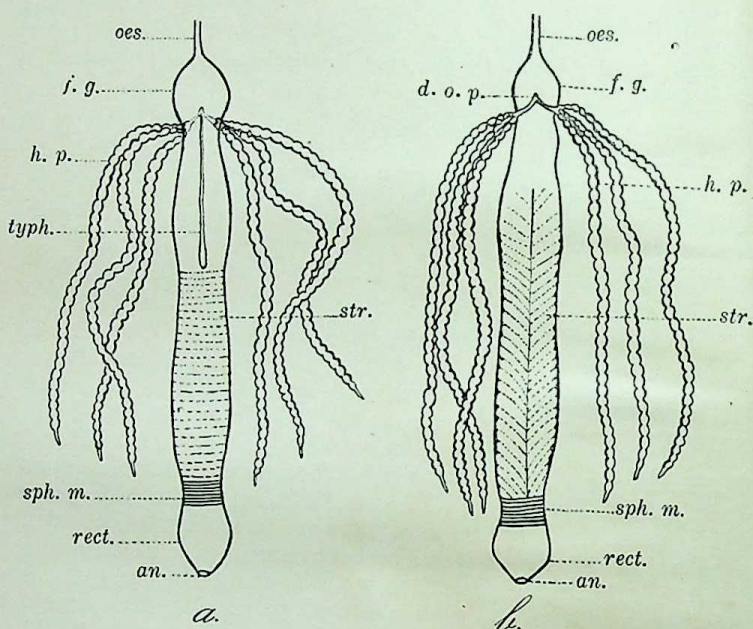


FIG. 1. a, Dorsal view of the Digestive Organs of *Ligia exotica*. b, Ventral view of the same. an., anus; d.o.p., dorsal opening of the common duct of hepato-pancreatic tubules; f.g., fore-gut; h.p., hepato-pancreas; oes., oesophagus; rect., rectum; sph.m., sphincter muscle; str., stratification of epithelium; typh., typhlosole. (\times cir. $2\frac{1}{2}$).

The intestine is a straight tube which presents special features along its dorsal and ventral aspects. The dorsal surface in both the genera is marked by a groove, more prominent in *Armadillio* than in *Ligia*. This groove extends from the anterior end to about half the length of the intestine in *Ligia* (fig. 1, a) and three-quarters in *Armadillio* (figs. 4 and 5) indicating an internal folding of the intestinal epithelium or the typhlosole.

In *Ligia* the epithelium of the posterior half of the intestine is disposed ~~biseri~~serially on either side of the mid-ventral line, giving it a characteristic pinnate appearance externally (fig. 2, b). The terminal portion of the intestine is marked by the presence of an extensive thick sphincter muscle, beyond which the intestine dilates into the rectum and opens to the outside through the anus.

The part of the gut between the opening of the hepato-pancreas and the beginning of the rectum is usually termed the 'midgut' in Isopods, but it is a misnomer since this part of the alimentary canal is not endodermal in origin. Embryological work on Isopods has shown that 'the digestive tract is formed almost entirely from two ectodermal invaginations (viz. the stomodæal and the proctodæal), the mesenteron being represented principally by the hepato-pancreatic lobes, only a very small portion of the intestine, just where the hepato-pancreatic lobes unite with it, being possibly endodermal' (10, 1895).

3. THE HISTOLOGY AND CYTOLOGY OF THE INTESTINE AND THE HEPATO-PANCREAS.

(a) *The Intestine.*

To study the histology of the digestive system, the animals were dissected alive in a fixing fluid or in normal saline, so that very little time was allowed for post-mortem changes. Bouin's, Carnoy and Corrosive sublimate were used as fixatives and these with Iron-hæmatoxylin invariably gave excellent results. For a more detailed study of cell-inclusions, Flemming's, Champy Kull, Ciaccio's, Da Fano, Nassanov, and Weigel's modification of Mann Kopsch were employed with satisfactory results.

Nicholls describes in full detail the fore-gut of *Ligia oceanica* (12, 1931). He finds that this chamber is equipped with a complicated armature of ampullæ and lamellæ for the extraction of liquid food, and that it has a filtering apparatus to strain the liquefied filtrate from the solid particles. He further adds that in *Ligia oceanica* the intestine and hepato-pancreas can absorb only liquefied food, a point which has been confirmed by me in *Ligia exotica*.

The fore-gut passes into the intestine which possesses the typhlosole in its anterior region. In a transverse section, the wall of the intestine presents the following layers beginning from the coelomic side (figs. 2 and 3) : (1) a discontinuous layer of longitudinal muscle-fibres, (2) a continuous layer of circular muscle-fibres, (3) a thin basement membrane, (4) the intestinal epithelium, and (5) a thick internal cuticular layer or intima.

The muscular layers are not sharply marked off; as a matter of fact, both the longitudinal and circular layers usually interlace so that it is difficult to make out their independent

existence. The basement membrane is thin but very definite. The epithelium forms the most important layer and is made up of a single layer of cells. The cells are demarcated by large

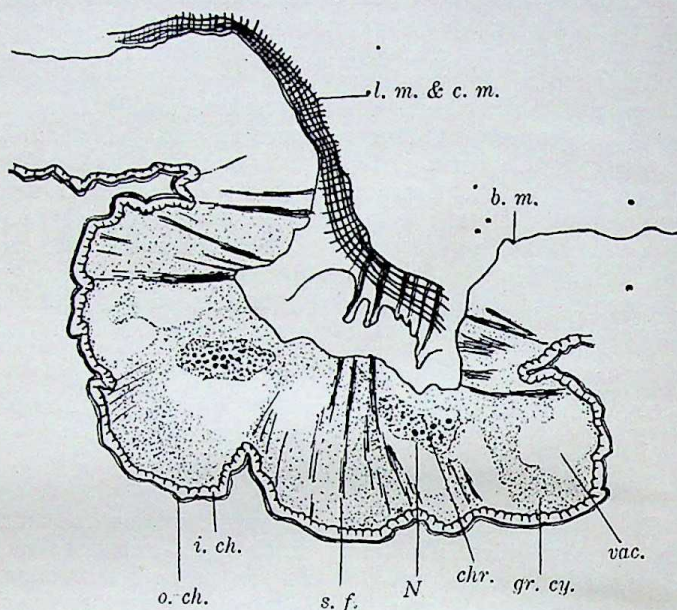


FIG. 2. A transverse section of the typhlosolar region of the intestine of *Ligia exotica*. *b. m.*, basement membrane; *c. m.*, circular muscles; *gr. cy.*, granular cytoplasm; *i. ch.*, inner chitin; *l. m.*, longitudinal muscles; *N.*, nucleus; *o. ch.*, outer chitin; *s. f.*, supportive fibres; *vac.*, vacuoles. ($\times 600$).

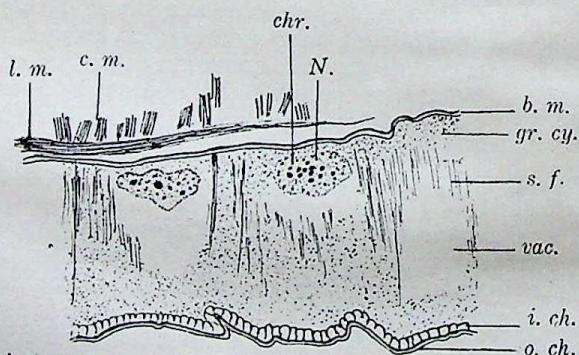


FIG. 3. A transverse section of the intestine of *Armadillio* to show details of histology. Letters as in fig. 2. ($\times 600$).

nuclei, the intervening cell-walls being absent. This feature had been observed by previous workers like McMurrich and Murlin in

other Isopods also, and they have described the epithelium as a 'syncytium'—a feature undoubtedly present in *Ligia* and *Armadillio*.

The structure of the intestine in *Ligia* and *Armadillio* presents several interesting features. Firstly, the typhlosole is most prominent in *Armadillio* and forms an infolding of the epithelium, extending laterally on either side into the lumen of the intestine like two horns (fig. 5); in *Ligia exotica*, on the other hand, the typhlosole is poorly developed (fig. 2). Secondly, the relative thickness of the epithelium varies in the two genera: in *Armadillio* the intestinal epithelium at the anterior end of the mid-gut is thinner on the dorsal and lateral sides, but enormously thicker on the ventral wall, about three times as thick (fig. 5). Posteriorly this thickness diminishes gradually till the epithelium on all sides is of a uniform thickness. The significance of this variation is not well understood; perhaps it is correlated with the greater degree of absorption in the anterior region. In *Ligia* the dorsal region of the intestinal epithelium is thrown into folds on either side of the typhlosole but there is no marked difference in the thickness of the cells in this region. Posterior to the typhlosole, however, there is a ventral groove, which is easily visible on a dissection of the entire gut. This groove is formed by a curving in of the intestinal wall, the cells on either side being longer and closely packed, thus giving a characteristic pinnate appearance externally.

In the syncytial epithelium of the intestine, the distribution of nuclei shows very clearly the cellular limits. In many places the basement membrane is lifted up between the two neighbouring cells and the internal cuticular lining of the cells is drawn in between the two adjacent cells. The epithelium is further characterized by the presence of 'supportive fibres'—'longitudinal thickenings of the cytoplasm—running from the basement membrane to the cuticular layer, which are all that suggest something of the nature of the cell-walls, but are indeed more (numerous?) than the nuclei' McMurich (10, 1898). The supportive fibres are disposed in bundles and are abundant in the typhlosolar region. In between the fibres the cytoplasm is granular and big vacuoles are seen prominently towards the intima. It is possible that both vacuoles and granules may be concerned with absorption in the intestine. The nuclei are large and spherical, often oblong and even amoeboid, with a clear nuclear membrane and a large number of chromatin granules. The nucleoli are also seen in a few cells.

The internal cuticle is surprisingly thick but without pores, although Murlin (11, 1902) is of opinion that in land Isopods the intima is provided with microscopic pores, while McMurich and Nicholls failed to establish the occurrence of these pores. I agree with the two latter authors, as I have also failed to see any pores in my numerous preparations. The cuticle is definitely

composed of two layers, of which the inner is thicker and contains many closely set cavities, while the outer is thinner and homogeneous.

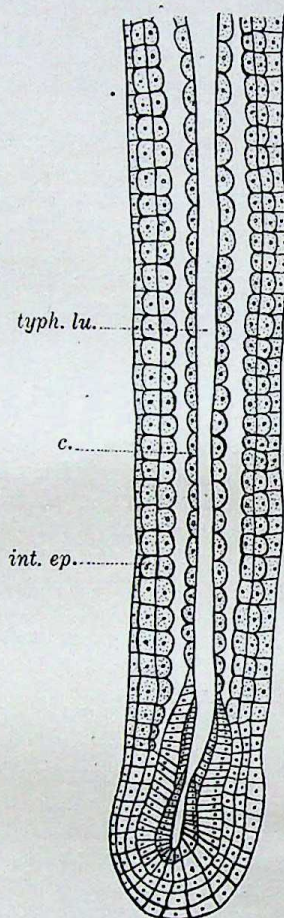


FIG. 4. A surface view of the typhlosome in *Armadillio c.*, cells bordering the groove of the typhlosome; *int. ep.*, intestinal epithelium; *typh. lu.*, lumen of the typhlosome. (\times cir. 26).

An interesting but obscure feature of the histology of the gut is that both in *Ligia* and *Armadillio* certain structures called 'blisters' are present on the wall of the gut. These are found usually in animals which have had a good meal before being killed. On sectioning the intestines of such forms, it is observed that the intestinal epithelium undergoes profound changes in the blistered portions. The internal cuticular layer gets separated off from the overlying cytoplasm which is filled up

with densely crowded and deeply staining granules. The supportive fibres are very scanty or even absent, and when present are found to be attached to the basement membrane alone in broken bits. The nuclei are unaffected and either occupy the

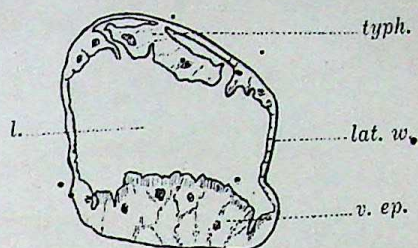


FIG. 5. A transverse section of the intestine of *Armadillio*. l., lumen of the intestine; lat.w., lateral wall of the intestinal epithelium; typh., typhlosole; v.ep., ventral epithelium. ($\times 266$).

usual basal position or move up to the luminal border. The great increase in the granules of the cytoplasm and the absence of supportive fibres are notable features and are undoubtedly related to some phase of absorption by the cytoplasm, 'the true significance of which is not understood yet' (12, 1931). Nicholls reports the same phenomenon in *Ligia oceanica* and it is stated that in the intestine of insects this is a phenomenon of common occurrence (Imms) and in fact in all articulated animals (Pavlovsky).

(b) *The Hepato-pancreas.*

A study of transverse sections (figs. 7 and 8) shows that the hepato-pancreatic cells are supported by a basement membrane and are surrounded by a muscular layer which controls the rhythmic movements of the glands. Externally each tubule is protected by a serous membrane which is thin and structureless and often peels off from the underlying layers in fixation.

The hepato-pancreatic gland consists of two types of cells: (1) tall columnar cells which are found in large numbers, and (2) wedge-shaped cells, which are small in numbers and are distributed among the cells of the first type. Each cell has its own thick cuticular wall, the chitinous nature of which has been verified by Patrick (14, 1927) by using the specific test of Pantin and Rogers for chitin.

The tall columnar cells have narrow bases where the nuclei are lodged. The nucleus is large and has a clear definite nuclear membrane; the chromatin granules are large and numerous; the nucleoli are prominent, their number varying from one to several. The cytoplasm is conspicuously alveolar, the alveoli being of varying sizes, the larger alveoli being found towards the luminal border. In fresh glands these cells are found to contain

yellow oil globules apparently of the nature of fat. On treatment with Sudan iii the yellow globules turned red, thereby showing the lipoidal nature of the globules.

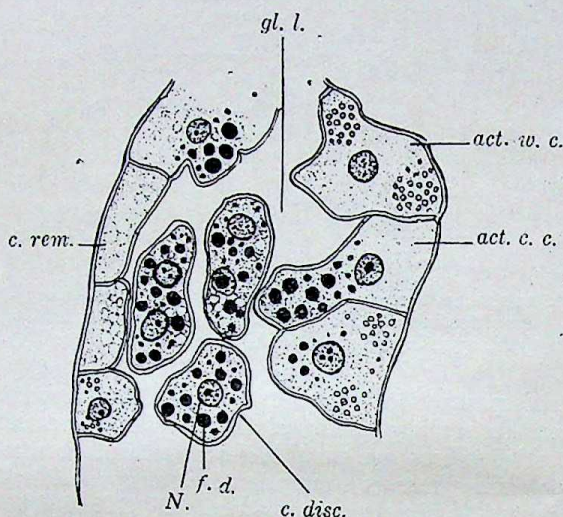


FIG. 6. A transverse section of the hepato-pancreas of *Armadillio* to show lipoidal secretion. *act.c.c.*, active columnar cells; *act.w.c.*, active wedge-shaped cells; *c.disc.*, cells discharged; *c.rem.*, cell-remnant; *f.d.*, fat droplets; *gl.l.*, lumen of gland; *N.*, nucleus. ($\times 266$).

In fixatives like Bouin's, Carnoy's and Corrosive sublimate, the vacuoles stand out well-defined. To determine the nature of these vacuoles precisely, tissues were fixed in Flemming and Champy Kull. In these osmic preparations the cytoplasm is found to be loaded with black globules in these vacuolar areas (fig. 8). When treated long with xylol or with turpentine, these black globules dissolve away leaving the vacuoles clear, as in Bouin's and Carnoy's fixatives. The blackening with osmic acid shows the fatty nature of the products in these vacuoles; also the fact that xylol can dissolve the fat shows that this fat is of the neutral type. Therefore these cells are proved to be concerned with the absorption and storage of fat.

As regards the wedge-shaped cells they are found to be more granular in all fixatives as compared with the columnar cells. These granules are finely distributed around the nucleus and stain intensely with Iron-haematoxylin. Besides these, larger granules are also present in these cells which are glistening in appearance and are yellowish brown in colour. They hardly take any stain and have been identified as *zymogen granules* of the hepato-pancreas, bodies which are concerned with the production of enzymes (fig. 8). These are very much more

conspicuous in *Armadillio* than in *Ligia*. Perhaps the complete terrestrial habit and consequent change of food may be the reason for increased enzyme production in the former.

Zymogen granules have been detected by Murlin, McMurrich, Frenzel and Nicholls, who all agree in their description of these granules. Patrick too identifies refringent granules in these cells, but comes to the conclusion that they are granules of mucin or its precursor *mucigen*. To test the correctness of Patrick's statement histo-chemical test for mucin was employed. Glands were fixed in corrosive sublimate and stained in specific stains for mucin such as Thionin, Toluidin blue, Mucicarmine and Methylene blue. Thionin and Methylene blue gave the best

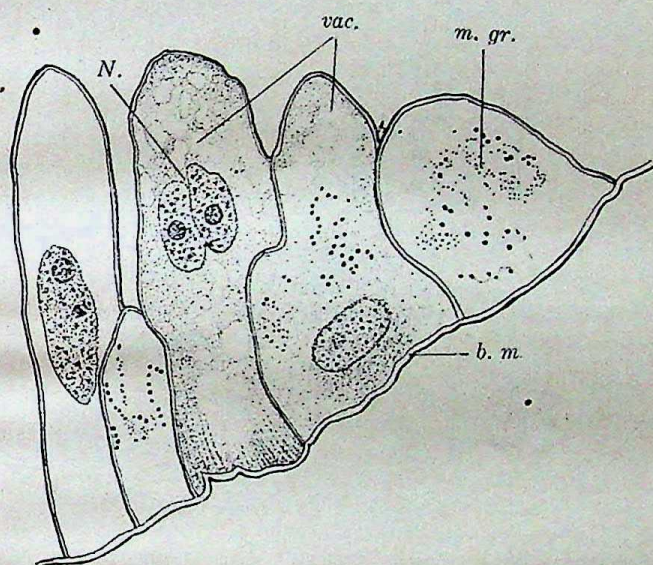


FIG. 7. A transverse section of the hepatopancreas of *Ligia* (Corrosive sublimate and Methylene blue) *b.m.*, basement membrane; *m.gr.*, mucin granules; *N.*, Nucleus; *vac.*, vacuoles. ($\times 600$).

positive results, mucin granules being stained reddish purple. It is absolutely clear, therefore, that mucin granules are present in these cells. But are they the yellowish brown, refringent granules of other preparations? To solve this problem, sections of glands in various fixatives were carefully compared. Zymogen granules are found to be best preserved in all osmic preparations, partly in Ciaccio's and hardly in corrosive sublimate. They are formed of complex chemical substances that stain with great difficulty. Acid fuchsin and Methyl green stain them red and they can thus be differentiated from the mitochondria which take up a purple colour with these stains. These observations corro-

borate those of Murlin's. Now, considering that the yellow granules are not preserved by corrosive sublimate, in which mucin specific stains react best, how can Patrick conclude whether they are granules of mucin or mucigen? I have tried to stain the zymogen granules, where they are preserved, in Methylene blue, in which they are found to take up a blue colour, but not the characteristic metachromatic purple stain, which Methylene blue imparts to mucin granules. We come to the problem again. Are both these granules the same, or are they two different inclusions in the hepato-pancreatic cells? My opinion is that they are entirely different cell-inclusions. Mucin is undoubtedly

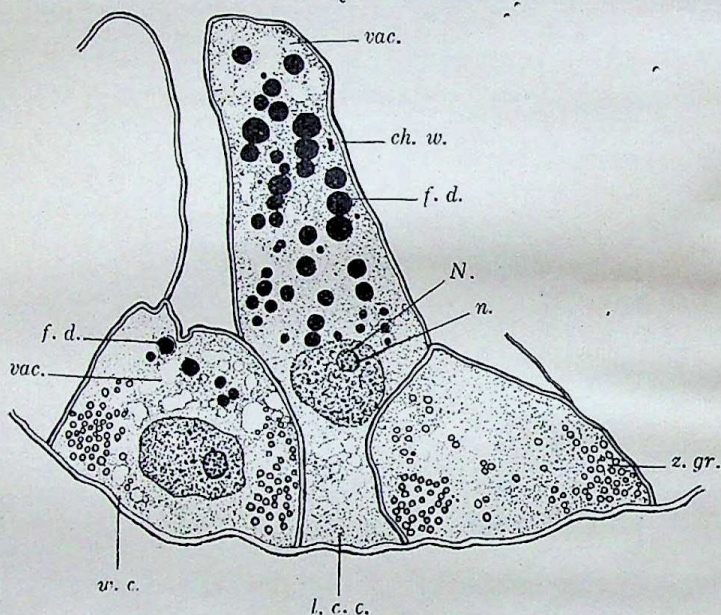


FIG. 8. A transverse section of the hepato-pancreas of *Armadillio* (Champy-Kull and Acid Fuchsin). *ch.w.*, chitinous wall; *f.d.*, fat droplets; *l.c.c.*, large columnar cells; *n.*, nucleoli; *z.gr.*, zymogen granules. ($\times 600$).

produced by the wedge-shaped cells and most probably helps to carry the zymogen granules (fig. 7).

Besides these granules, fat globules are also found occasionally in the wedge-shaped cells both in *Ligia* and *Armadillio*. We have already observed the occurrence of a large amount of fat in the tall columnar cells. What is the origin and distribution of fat in the hepato-pancreas? To settle this point, glands were fixed in Ciaccio's mixture for lipoids and stained in Sudan iii. When examined it was found that lipoidal granules, stained orange-yellow, occur in both columnar and

wedge-shaped cells, showing thereby that both types of cells manufacture lipoids and the distinction as raised by Webber and supported by Patrick is untenable.

Frenzel, Murlin and Nusbaum consider that the smaller cells are the young stages in the cellular growth of hepato-pancreas. The last author thinks that the wedge-shaped cells are more concerned with enzyme production, although fat is also synthesized in them to a small extent, while in the columnar cells, fat accumulates so as to fill up the cells, and that little or no zymogenesis occurs in these cells. My observations confirm these conclusions of Nusbaum.

4. THE PHYSIOLOGICAL ACTIVITIES OF THE INTESTINE AND THE HEPATO-PANCREAS WITH SPECIAL REFERENCE TO ABSORPTION.

Since both the intestinal epithelium and the cells of the hepato-pancreas are lined with a chitinous cuticle, the problem of absorption has been of great interest to all workers on the digestive system of Isopods. To summarize the work already published on this point we might mention the following:—

(I) McMurrich (1898) is of opinion that the 'midgut' of Isopods does not play any part in absorption but that it serves as a reservoir of food. It is the hepato-pancreas that is both digestive and absorptive, a statement for which he does not adduce any experimental evidence.

(II) Murlin (1902) thinks that the cuticle is porous and gives experimental evidence to show that fat and certain albuminous substances are absorbed through the epithelium of the intestine. He also says that a microscopical study of the absorption of fat indicates that fat is hydrolysed by digestive enzymes and that it is absorbed in the form of cleavage-products and at least partially synthesized into neutral fat under the influence of ferment action. But he also does not adduce any experimental proof.

(III) Nusbaum (1917), by feeding the animals on Ferrie peptonate and staining the sections with Potassium ferrocyanide and Hydrochloric acid, found that both the intestine and hepato-pancreas were absorptive.

(IV) Aubery Nicholls (1931) working on *Ligia oceanica* at the Plymouth Laboratory reports that he has been able to demonstrate that the 'midgut' throughout its length and the hepato-pancreas are both absorptive. He followed Yonge's method (1926, b) and fed the animals on colloidal iron in the form of Ferrum oxydatum saccharatum. After a given period, the gut and hepato-pancreas were fixed in 5% solution of ammonium sulphide in 90% alcohol, to which an equal quantity of Bouin's fluid was added. The sections were then treated with a 10% aqueous solution of Potassium ferrocyanide followed by a

few minutes in a dilute solution of Hydrochloric acid, and a bright Prussian blue colouration resulted wherever the colloidal iron had been absorbed. In the hepato-pancreas the absorbed iron was found to aggregate around the zymogen granules.

In order to investigate the range of absorption in *Ligia exotica*, I first fed the animals with powdered carmine, and at varying intervals, ranging from 2-38 hours, dissected the alimentary canal, fixed and sectioned it. I found that carmine could be detected only in the lumen of the gut and nowhere else in the digestive tract, the particles being ejected through the anus. Patrick tried this method to test the excretory rôle of hepato-pancreas and she came to the conclusion that the glands did not serve an excretory function, a conclusion with which I agree.

On feeding the animals with olive oil stained red with Sudan iii, it was found on dissection and examination of fresh tissues under the microscope, that the whole of the intestinal epithelium and the hepato-pancreas were coloured red with the absorbed oil-globules.

Yonge's method was also employed, but was only partially successful as the colloidal iron in that nutritive form was not available. However, it was seen by this method also that the cells of the hepato-pancreas and the intestinal epithelium have powers of absorption.

The phenomenon of absorption was corroborated by feeding the animals on medicinal Methylene blue and Neutral red. It is a well known fact that certain dyes like Methylene blue and Neutral red stain tissues in their vital condition, and if these are absorbed by the intestinal epithelium and hepato-pancreas, the absorbing cells will indicate the presence of granules of these vital dyes. In order to study, therefore, the physiology of absorption, specimens of *Ligia* were fed on bread, soaked in dilute solutions of medicinal Methylene blue overnight. When these animals were dissected out, it was found that the intestine was stained blue throughout its length; they were, therefore, kept in Ringer's solution and examined under the microscope.

The syncytium of the intestine was stained pale blue, while the nucleus was deep blue and the nucleolus had taken an intense shade of blue. But the most significant point is that granules of Methylene blue could be detected in the cytoplasm around the nuclei, which no doubt demonstrates that the intestinal epithelium is absorptive.

The hepato-pancreas afforded interesting results with regard to the absorption of this vital dye. The lumen of each gland contained granules stained greenish yellow. The wedge-shaped cells of the smallest size were filled with purple grains all round the nuclei recalling very clearly the characteristic stain for mucus in corrosive sublimate preparations, but no fat-globules were found in them, while other cells of the same category but slightly

bigger were found to contain a good number of fat-globules but the purple-grains were scanty. Finally, the tall columnar cells were entirely filled with fat droplets but no Methylene blue grains.

Neutral red had been employed by Covell (5, 1928) to study the pancreatic secretion of the guinea-pig in the living state. A similar attempt was made by me in *Ligia*, but these animals are too fragile to withstand long experimental studies. Animals were fed on Neutral red (1% solution) for an hour and were then dissected alive, keeping the hepato-pancreatic tubules in Ringer's solution. The distribution of absorbed Neutral red granules was noted under the microscope.

It was observed that both kinds of cells were absorptive; but the degree of absorption varied. The smaller cells were filled with Neutral red granules all around the nuclei but there were few or no fat-globules, but in some of the other cells both fat and Neutral red granules were found together. In the columnar cells only fat-globules were seen, recalling the results of experiments with Methylene blue.

To corroborate these observations, the glands and the gut of animals fed on Neutral red were fixed in Turchin's fluid, so that the absorbed dye could be preserved and fixed. In sections it was found that the cytoplasm of the hepato-pancreatic cells was stained pale pink towards the inner cuticular border. Certain vacuoles containing Neutral red granules were found between this border and the nucleus, thus confirming the phenomenon of absorption.

5. THE SECRETORY FUNCTION OF THE HEPATO-PANCREAS.

The trend of modern cytology in glandular secretion is directed towards the Golgi apparatus. Interesting and far-reaching results have been obtained on various glandular tissues by Nassanov, Bowen, Brambell, Gatenby, Ludford and Cramer. According to Bowen it has been clearly established that an intimate topographical relationship exists between the Golgi material and the secretory products.

In order to investigate the activity of the cells in the manufacture of secretory products, glands were fixed in Nassanov's and Weigel's modification of Mann Kopsch for Golgi bodies, mitochondria, secretory granules and the nuclear apparatus. Both these osmic preparations give identical results and Golgi apparatus was found to hold a close relationship with the secretory vacuoles of fat, indicating probably that the latter arise in relation to the Golgi bodies. But the exact details of synthetic operation have still to be investigated.

The origin of zymogen granules is still problematical. Nassanov's and Da Fano's preparations have shown that they are found in topographical relationship with Golgi bodies in the

wedge-shaped cells, but this conclusion is only tentative and needs further critical evidence.

The secretion of the hepato-pancreas in Isopods is essentially lipoidal in nature and presents certain characteristic features. We have noted that the columnar cells are the mature phase of cellular growth and that it is these that are concerned with the discharge of secretory products. These cells are cut off from their basal portions either without the nuclei or with the nuclei, in which case they are intact and fall into the lumen carrying the secretory products of fat, enzymes produced by the zymogen granules, and the disintegrated Golgi material (fig. 6). These products are then pumped into the intestine by the rhythmic contractions of the glands where they react on the liquid food absorbed. This statement is substantiated by the presence of discharged cells in the intestinal tract. The fate of these fat-globules is little understood at present. In this connection we come to the much disputed question of the types of cell and cell-differentiation in the Isopod hepato-pancreas. Webber is of opinion that the long columnar cells are morphologically and physiologically different from the smaller wedge-shaped cells. Later workers like Frenzel, Murlin, and Nicholls hold that their apparent differences are due to their different stages of growth. Patrick, on the other hand, identifies the long columnar cells as 'fat-secretory and storage cells', and the wedge-shaped cells as purely 'mucous cells', a statement which has been proved to be untenable.

Microscopical examination of the glands-cells alone cannot give a conclusive proof for one or the other view, for cells are not physico-chemical entities alone, but are, above all, biological and physiological. Therefore, I attempted to examine the cells under experimental conditions of absorption of Methylene blue and Neutral red. It has already been pointed out that the smaller cells are indicative of great absorption, the larger ones of little or none, while the intermediate ones are partly absorptive and partly secretory. I, therefore, come to the conclusion that the cells of the hepato-pancreas show progressive stages of growth and differentiation, the smaller cells being at first enzymatic and mucus-secreting with a great power of absorption, and that later they become fat-secreting and storing. I hope that a critical study of the Golgi apparatus in these cells will clear our doubts about the morphological differentiation and the physiological rôle of these cells and this point has to await further work.

6. SUMMARY.

I. The intestinal epithelium and the hepato-pancreas of the two Isopods, *Ligia exotica* and *Armadillio elevatus*, are both absorptive.

II. The differences in the cells of the hepato-pancreas are due to their different stages of growth. The smaller cells are primarily enzymatic and mucus-secreting to begin with, but later develop into columnar cells which are predominantly fat-secreting and storing.

III. The fat globules are secreted in vacuoles found in relation with the Golgi material, the latter being, therefore, concerned with fat-secretion in the cells.

IV. The secretion of the glands is typically lipoidal in character, the nuclei remaining intact in the cells, which are discharged 'in toto' into the lumen of the gut.

V. Zymogen granules have been found to arise in relation with the Golgi apparatus in the wedge-shaped cells and they indicate that these cells are physiologically more active in absorption and intra-cellular digestion.

7. ACKNOWLEDGMENTS.

It gives me great pleasure to express my sincere thanks to Professor R. Gopala Aiyer, Director of the Zoological Laboratory, University of Madras, for his interest and help during the short period of my work, and to Professor K. N. Bahl of the Lucknow University for his suggestive and critical revision of my paper.

Also I wish to express my deep gratitude to my Alma Mater, The Women's Christian College, Madras, for granting me the post-graduate scholarship to carry out this work.

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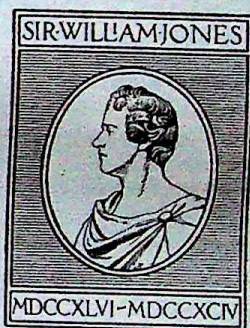
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CALCUTTA:—Published by the Royal Asiatic Society of Bengal, and Printed
by P. Knight, Baptist Mission Press, 41A, Lower Circular Road.

JOURNAL
OF THE
ROYAL ASIATIC SOCIETY OF BENGAL
SCIENCE
Vol. IV, 1938, No. 2



CALCUTTA

PRINTED AT THE BAPTIST MISSION PRESS
PUBLISHED BY THE ROYAL ASIATIC SOCIETY OF BENGAL, 1, PARK STREET

Issued November, 1939

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Journal Royal Asiatic Society of Bengal. Science.

Volume IV, 1938.

ARTICLE No. 2.

Some Recent Advances in Insect Embryology, with a Complete Bibliography of the Subject.

By MITHAN LAL ROONWAL.

(Communicated by Dr. B. Prashad.)

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I. INTRODUCTION.

After a lull during the second decade of the twentieth century, interest in insect embryology is to-day showing signs of revival. This is to be welcomed as, notwithstanding the enormous amount of work done on this subject—nearly 700 references have been listed at the end of this account—, certain outstanding problems are still productive of much divergence of opinion. The process of gastrulation, the origin of the mid-gut epithelium and, in short, the general problem as to how far the classical germ layer theory is applicable to insects, are matters of dispute to-day. Recent work has provided satisfactory solutions for at least some of these problems. Moreover, the discovery of the labral and preantennary pairs of coelomic cavities by WIESMANN (1926) in *Carausius*, and the confirmation of the former by MELLANBY (1936) in *Rhodinus* and by ROONWAL (1937) in *Locusta*¹ has lent a new interest to the problem of head segmentation among Arthropods in general and insects in particular. These and other discoveries have tended to support, on very strong embryological evidence, the 7-segmental nature of the insect head and this view is, therefore, presented in the following account. A new interpretation of the insectan protocerebrum in support of the same view is also given. Advance in our knowledge has been made in several other fields also, such as those relating to the abdominal appendages, the embryonic membranes, the provisional dorsal closures, the embryonic blood sinuses, etc., and all these structures are dealt with briefly.

Owing partly no doubt to the large amount of yolk in the insect egg, its early embryological development has become extremely distorted and, therefore, difficult of interpretation, especially in matters relating to the formation of the germ layers. At the same time it cannot be emphasized too strongly that the first essential for a correct approach to the solution of the various controversial points is to employ the very highest standard in the technique both of the handling of material and of actual observation. Given the former, the one requisite most needed is a complete freedom from theoretical prejudices. A perusal of the original papers indicate that not a few embryologists have failed in this quality. Regarding the technique of the handling of material, two requirements are essential. These are: (1) Good fixation and proper sectioning. For example, an artificial space in mesodermal tissues, caused by bad fixation, might easily, but wrongly, be interpreted as a coelomic cavity. (2) Accurate timing of the embryonic stages. Eggs, from the moment of laying, must be incubated at constant temperature and humidity, and examined at regular and short intervals of

¹ Also in *Pteronarcys* by MILLER (1939), see Appendix, p. 105.

time. While this procedure ensures accurately timed stages, a word of caution is necessary lest the embryologist should rely solely on this method. It has been found (WIESMANN, 1926; SLIFER, 1932, b) that even under a uniform external environment, the rate of development in the same egg-batch may vary from egg to egg within fairly wide limits. As pointed out by WIESMANN, such characters as the number of segments differentiated, the first appearance of the proctodæum (and the stomodæum), the beginning of the differentiation of the fat body, etc., provide supplementary and often more accurate criteria than a temperature-time scale for determining the developmental stage of the embryo. Even so it is not always possible to draw a sharp line between one developmental period and another. In short, the embryologist must be certain that he has missed no developmental stage, however insignificant and unworthy of record it might seem to him from his previous theoretical knowledge. Failure to satisfy this requirement—because the older embryologists incubated their eggs either in the room or in the open, where environmental conditions fluctuate considerably—was often the cause of overlooking several fleeting but nevertheless important phenomena, as, for example, the supernumerary ventral (gastral) grooves which are probably of a much more general occurrence among insects than has hitherto been admitted. Thus, in *Locusta* two ventral grooves are formed of which the first one lasts for less than 4 hours (at 33°C.), and the second one, which appears a few hours later, also lasts for an equally short period. On the other hand, the fulfilment of the above requirements in several recent papers has produced results of considerable value.

Finally, it is a pleasure to acknowledge my indebtedness to DR. BAINI PRASHAD, Director, Zoological Survey of India, for his kindness in critically going through the manuscript and suggesting many improvements, and for correcting the proofs.

II. HISTORICAL.

ARISTOTLE, in the last three-quarters of the fourth century B.C., had noted that some insect eggs have 'soft shells' and increase in size after being laid. Such eggs he termed as 'imperfect' in contradistinction to 'hard-shelled eggs', such as those of birds, which do not so increase in size. He, however, regarded the chrysalis also as an egg stage. The increase in size of insect eggs was re-discovered several centuries later by RATHKE (1844) in the eggs of the mole-cricket, *Gryllotalpa vulgaris*, and some of the caddis flies or Trichoptera (vide ROONWAL, 1936, a)¹. FABRICIUS (1687) 'marks a definite

¹ It is of interest to note in this connection that SLIFER (1938, a) has recently discovered in the egg-membrane of the grasshopper,

advance upon ARISTOTLE when he says that silk worms and other insects are born into their larval state from an egg, though he still terms the chrysalis an egg, and therefore holds that they are generated twice' (N., pp. 87-89). HARVEY, in the first half of the seventeenth century, believed in *Omne vivum ex ovo*¹, implying that even the most imperfect and lowest animals are born from eggs and not by spontaneous generation. He writes, 'We shall show that many Animals themselves, especially insects, do germinate and spring from seeds and principles not to be discerned even by the eye, by reason of their contract, invisible dimensions . . .' (N., p. 122). Unfortunately, his further notes on the generation of insects were destroyed in his house in London at the time of the Civil War. HARVEY, like ARISTOTLE, was an ardent epigeneticist. The final death blow to the idea of spontaneous generation was given by REDI (1688) whose work must consequently remain, although indirectly, the starting point of developmental studies on all minute oviparous invertebrates. MALPIGHI (1669), the 'principal glory' of the 'micro-iconographic' school, and SWAMMERDAM (1737) were largely concerned with the larval and adult anatomy of the silk-worm, honey-bee and other insects, and their few observations on insect eggs are not of much importance from the purely embryological point of view²; both these authors were preformationists. LEEWENHOEK (1695) made some interesting observations on the eggs of fleas.³

After this there is a long gap of over a century during which no observations were made on insect embryology. However, for comparative animal embryology as a whole, it was a most important period, for during it the germ layer theory was slowly taking shape. In the formulation of this theory, there stand

Melanoplus differentialis, a special water-absorbing area which she calls the 'hydropyle'. This area is located in the 'yellow cuticle' at the posterior or micropylar end of the egg. The egg absorbs water from outside largely through the hydropyle.

¹ This pithy saying itself is, however, not attributable to HARVEY. Nor is it strictly correct in the light of later advances in our knowledge. The Protista, for example, do not produce eggs.

² SWAMMERDAM, however, rendered great service by observing and figuring the eggs of a large number of insects, including the body-louse, dragonflies, mayflies, honey-bee, humble-bee, ants, and several beetles and moths. In the middle of the developing egg ('nit') of the louse he observed a small area showing heart-like pulsations; this he called the 'pancreas' as 'it moves up and down with the stomach'—presumably he was observing either the bulbus arteriosus or the peristalsis of the lateral body-walls in the late embryo.

³ The substance of this paragraph, giving the early history of insect embryology, is largely taken from Dr. J. NEEDHAM's excellent book *A History of Embryology* (1934), and the quotations taken therefrom are acknowledged with the suffix N., followed by the page of the book. For references to the embryological works of ARISTOTLE, FABRICIUS and HARVEY, the same book should be consulted.

out prominently the works of WOLFF (1759) and PANDER (1817), culminating in the classic book of VON BAER (1828).

The first clear reference to early insect embryos was probably that by SUCKOW (1818) who observed that in the eggs of *Bombyx (Gastrophaga) pini* (Lepidoptera) a small dark spot is formed in the centre of the originally clear yolk. This he rightly regarded as the early embryo (germ disc), but, as BURMEISTER (1832) later pointed out, the embryo or ventral plate lies on the surface of the yolk, not in the centre. SUCKOW also observed the serosa, the alimentary canal, the tracheæ, the dorsal vessel, the central nervous system and finally, the gonads in the late embryo. The next contribution was that of RATHKE (1832), contained in a small paper of eight pages exclusively devoted to the embryology of the cockroach, *Blatta orientalis*. He examined embryos dissected out of the egg, but did not cut sections. This was soon followed by the works of KÖLLIKER (1842) and RATHKE (1844).

The intensity of the active period which followed¹ was heightened by the invention of the microtome in about 1860 and, with it, the rapid development of the section-cutting technique. Authors who made special contributions during this period are mentioned below; in their earlier works they did not study sections, but later they employed that technique:—WEISMANN (1863–1882), METSCHNIKOFF (1865–1875), BALBIANI (1866–1885), DOHRN (1866–1876), GANIN (1869–1874), BRANDT (1869–1880), and others. KOWALEWSKY (1871–1886) first studied insect embryology by cutting sections and thus laid the foundation of much of our knowledge of the subject as understood to-day, and it was BOBRETZKY (1878) who first followed the process of cleavage in large yolk-laden eggs with the help of sections. All these authors dealt with pterygotan insects. It was, however, during the last decade of the nineteenth century and the first decade of the twentieth that activity was most intense and the greatest amount of work on insect embryology was done. No doubt, this was due partly to the development of a tolerably satisfactory technique of section-cutting and staining, for insect eggs, like all others eggs which are rich in yolk, are notoriously difficult to section. It is impossible to mention all the authors in this review, and only a few whose contribution has been the greatest will be referred to. Two of the greatest masters of insect embryology, viz., GRABER (1877–1891) and HEYMONS (1890–1912), deserve first mention. The brilliant and remarkably penetrating studies of GRABER dealt with an extensive series of pterygotes, including the Orthoptera, Odonata, Hemiptera, Trichoptera, Lepidoptera, Coleoptera,

¹ For a detailed review of this period up to 1897, consult LÉCAILLON (1898, a).

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Hymenoptera, Diptera and others. To the insect embryologist, his original papers are indispensable even to this day. Next comes HEYMONS whose classical studies of the Orthoptera and Dermaptera, as well as his views on bi-phased gastrulation and the absence of a functional insectan endoderm, are well known. He also studied the Ephemeroptera, Odonata, Hemiptera and Thysanura (*Lepisma*), and his great work on *Scolopendra* (Chilopoda) may also be mentioned. Reference may now be made to some other important works, such as those of NUSBAUM (1882-1891); WILL (1883-1888) who first suggested the 'newer bi-phased gastrulation theory' for insects; CHOŁODKOWSKY (1888-1895); BLOCHMANN (1884-1895); HEIDER (1885-1897); HENKING (1888-1892); WHEELER (1889-1893); LÉCAILLON (1897-1898); and CARRIÈRE and BÜRGER (1897). The work of the last-named authors on the mason-bee, *Chalicodoma muraria*, is perhaps the most complete embryological account in existence of a single insect. Workers on the Apterygota, such as CLAYPOLE (1892; 1898), UZEL (1897-1898) and PHILIPTSCHENKO (1912), must also be mentioned, as well as those on the parasitic Hymenoptera, viz., MARCHAL (1897-1906) and SILVESTRI (1906-1921). In this period also appeared the well-known work of KORSCHOLT and HEIDER (1892-1910) on invertebrate embryology.

Coming to a more recent period, we have the works of HIRSCHLER (1906-1924) whose chapter on 'Embryogenese der Insekten' (1924) in Schröder's 'Handbuch der Entomologie' is undoubtedly the most comprehensive general account of insect embryology that has appeared in recent times. The second decade of the twentieth century did not prove very productive, partly owing no doubt to the intervention of the Great World War. The works of NELSON (1911-1918) on the honey-bee are, however, a notable exception. But in more recent times, interest in insect embryology has revived and we are having a large number of papers on the subject. Among them may be especially mentioned the works of GRANDORI (1911-1932) on *Bombyx mori*, coccids, etc.; BLEDOWSKI and KRAINSKA (1926) on the parasitic Hymenopteran, *Banchus femoralis*; the elaborate work of WIESMANN (1926) on coelom formation in the stick insect, *Carausius morosus*, Br. (Orthoptera); EASTHAM (1927-1930) on *Pieris rapae* (Lepidoptera); NOSKIEWICZ and POLUSZYNSKI (1928) on the parasitic genus *Stylops* (Strepsiptera); ROONWAL (1935-1939) on the African Migratory Locust, *Locusta migratoria migratorioides* R. & F. (Orthoptera), and on gastrulation in general; MELLANBY (1935, 1936) on *Rhodnius* (Hemiptera); SCHLÖZEL (1937) on some Anoplura (including Mallophaga); and finally, TREGS and MURRAY (1938) on *Calandra oryzae* (Coleoptera). (Also see Appendix, p. 105.)

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III. SOME RECENT ADVANCES

1. TECHNIQUE.

The sectioning of the yolky eggs of insects has always been a difficult and laborious process, but the technique recently evolved by SLIFER and KING (1933) and modified by ROONWAL (1935, *a*) has made this task easy. Fixed eggs are cut into two transverse halves and soaked for 24 hours in a 1-4% solution of carbol-ic acid in 80% alcohol. They are then dehydrated in 95% alcohol, cleared in carbol-xylol and embedded, as usual, in wax (M.P. 52°C.) for 10-30 minutes according to the size of the egg. The wax block is then trimmed so as to expose the cut side of the egg and then soaked in water for 24 hours. The block then cuts very easily. The duration of soaking in carbol-ic acid solution, as well as in water, can be shortened to about 6 hours in a vacuum bath. A 4% carbol-ic acid solution is not always safe to use and a weaker strength is often preferable.

2. GASTRULATION AND THE GERM LAYERS¹.(a) *Theories of Gastrulation.*(i) *The older theories.*

Until recently, two main views existed in regard to the nature of gastrulation and the formation of the germ layers in insects. These are:—

1. A true blastula is present in insects and is formed when the cleavage cells reach the egg-periphery. Gastrulation occurs afterwards when the inner layer is differentiated. Yolk cells have no germ layer value. Endoderm is usually bipolar in origin. This view was advanced by KOWALEWSKY (1886) and supported by WHEELER, NUSBAUM and FULINSKY, STRINDBERG, and more recently by EASTHAM (1927; 1930, *a*, *b*), THOMAS (1936) and others.

2. No blastula occurs, the so-called blastula of the first view being regarded as the first gastrulation stage. Gastrulation occurs in two stages. The interpretations of this view fall into two groups, thus:

(a) Older bi-phased gastrulation theory.—The first gastrulation phase is represented by the separation of the primary yolk cells from the other cleavage cells, and the second phase by the immigration of secondary yolk cells from the primary epithelium.

¹ For a review of the older literature on germ layer formation in insects, see EASTHAM (1930, *a*).

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Differentiation of inner layer is not a gastrulation act. Yolk cells alone represent endoderm, but, since they degenerate, no endoderm shares in the formation of adult body. Insectan mid-gut is ectodermal in origin. This theory was first clearly put forward by HEYMONS (1895, *a*; 1901), and supported by LÉCAILLON (1897-1898), SCHWARTZE (1899) and others.

- (b) Newer bi-phased gastrulation theory.—The first phase corresponds to the first phase of the older theory, but the second phase is represented by centripetal separation of yolk cells as well as by differentiation of inner layer. Primary epithelium is regarded as ectoderm, not blastoderm. Mid-gut epithelium is endodermal. This theory was first put forward by WILL (1888), but we owe its full exposition to HIRSCHLER (1912; 1924).

(ii) *The new theory of multi-phased gastrulation.*

This was suggested by ROONWAL (1936, *b*) in order to explain several embryological facts which were previously not explicable on the bi-phased gastrulation theories. Four phases were tentatively recognized in *Locusta*. More recently, the theory has been amplified (ROONWAL, 1939, *b*) and has been shown to be applicable not only to most insects but also to several other Arthropods. The essential features of the amplified theory are: (i) Blastula stage is suppressed in most cases. (ii) Gastrulation has undergone both temporal and spatial elongation, and become multi-phased. It generally occurs in three phases and numerous sub-phases of the first and second order. (iii) All the three germ layers have acquired a quadruple nature. We may distinguish in them firstly, primary and secondary portions. Secondly, each of these may contain permanent and evanescent portions. (iv) The primary germ layers tend to undergo various degrees of reduction and may even be totally suppressed. (v) Multi-phased gastrulation is brought about by a combination of the various modes by which uni-phased gastrulation generally occurs. (vi) The definitive mid-gut epithelium is generally a secondary formation belonging to the secondary endoderm. (vii) Yolk cells are endodermal in nature.

Recently, TIEGS and MURRAY (1938) have shown that the mid-gut epithelium in *Calandra oryzae* arises from the blind ends of the stomodæal and proctodæal invaginations. While this is only one more confirmation of what has been previously demonstrated by several authors in a variety of insects, it is the interpretation of this fact by TIEGS and MURRAY that calls for some remarks. They maintain that endoderm does not occur in the embryo of *Calandra*, and further generalize that 'when the gastral epithelium arises early, then endoderm forms; but when

it does not appear till much later, there is no endoderm'. One would naturally ask: What then is the validity of the well-established germ layer theory if endoderm may be altogether absent in an embryo? The answer to this question would seem to lie in the multi-phased gastrulation theory in its amplified form.

(b) *Some Structures connected with Gastrulation.*

Recently, some new and important structures have come to light in connection with insect gastrulation. At the same time, some of the older structures have either received new interpretations or been given new names in accordance with modern ideas on gastrulation. They are mentioned below.

Supernumerary ventral grooves.—One mid-ventral groove analogous, but not homologous, with the blastopore, is generally characteristic of embolic gastrulation. Recently it has become evident in insects that besides the main groove from the roof of which the inner layer is proliferated, other grooves are also formed, although these latter do not take an important share in the formation of the inner layer. Nevertheless, the supernumerary grooves constitute a strong support for the multi-phased gastrulation theory. In accordance with the time of their appearance, the grooves have been named by ROONWAL (1936, b) as the first, second and third ventral grooves, of which the second one is the main groove occurring in all embolic insects. The first ventral groove has been recorded in *Pieris* (EASTHAM, 1927), *Calandra* (INKMANN, 1933), *Locusta* (ROONWAL, 1936, b) and *Carausius* (THOMAS, 1936). The third ventral groove was recorded by KOROTNEFF (1885) in *Gryllotalpa*, but its significance was not appreciated, since neither the first nor the second groove occurs in this insect.

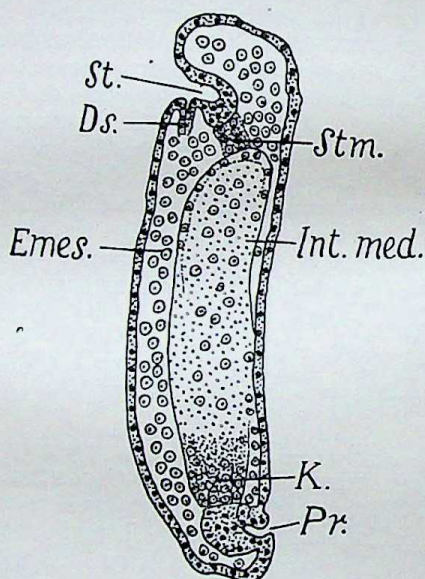
Primary epithelium.—This name has recently been given to the first cell-layer formed in insect eggs (ROONWAL, 1936, b). It is the so-called blastoderm of the older authors and the 'Oberflächenepithel' of HIRSCHLER (1924). It represents the ectoderm.

End-ectodermal masses.—The cell proliferations developing in many insects at the blind ends of the stomodæum and the proctodæum and forming the mid-gut epithelium, have been variously interpreted as purely ectodermal or purely endodermal. Since in ontogenic origin they are undoubtedly ectodermal and in phylogeny endodermal, they have been termed as 'end-ectodermal masses' (ROONWAL, 1939, b). They represent a portion of the secondary endoderm.

3. THE ALIMENTARY CANAL AND THE MALPIGHIAN TUBULES.

The true nature of the insectan mid-gut epithelium has been stated above, and I shall briefly describe here some new and recent conclusions regarding its actual mode of origin in

ontogeny. The share of the yolk cells in the formation of the mid-gut epithelium had been formerly shown only in two cases, viz., in *Lepisma* (HEYMONS, 1897, a) and the Libellulidæ (TSCHUPROFF, 1903). In both instances the accuracy of the observations has been doubted by other workers. It is, therefore, of considerable interest that more recent authors have found this condition in some other insects where the mid-gut epithelium is of a mixed origin. In *Bombyx mori* (GRANDORI, 1932, a) the mid-gut epithelium is claimed to arise from the ectoderm and yolk cells. In the Ichneumon, *Banchus femoralis*, BLEDOWSKI and KRAINSKA (1926) distinguish three sections of the mid-gut, viz., a middle yolk sac which forms the main portion of the mid-gut epithelium and, at either ends of the sac, a small 'stomodæal' and a small 'proctodæal' mid-gut (Text-fig. 1).



Text-fig. 1. Longitudinal section of the embryo of *Banchus femoralis*, showing the triple origin of the mid-gut epithelium. Semi-diagrammatic. (Adapted from BLEDOWSKI and KRAINSKA, 1926.)

Ds., ductus sericterii; Emes., inner (lower) layer; Int. med., mid-gut of yolk-sac origin; K., posterior cell-cap (rudiment of 'proctodæal' mid-gut); Pr., proctodæum; St., stomodæum; Stm., anterior cell-cap (rudiment of 'stomodæal' mid-gut).

The majority of the recent investigations point to an embryonic origin for the regeneration cells and nuclei of the mid-gut epithelium. BUSHNELL (1936) has made the interesting discovery that in the beetle *Acanthoscelides* the mid-intestinal epithelial cells of the late embryo are of two sizes. The larger ones form the functional larval epithelium, while the smaller ones become the

regeneration cells. The nuclei of the larger cells have nearly twice the volume and contain twice as many prochromosomes as those of the smaller ones—the volume and prochromosome number respectively being 195 cu. μ . and 40 in the former and 113 cu. μ . and 20 in the latter. This author further suggests that the nuclei of the regeneration cells may have a two-fold origin: firstly, from certain small cells which become isolated at the base of the mid-gut epithelium during early larval development; and secondly, from 'pseudo-reduction' divisions of the large nuclei in the larval epithelium.

Sometime ago, HENSON (1932) attempted to homologize the stomodæal and proctodæal invaginations of *Pieris* embryo with the oral and anal remnants of the blastopore of *Peripatus*. This ingenious view, along with HENSON's idea of the endodermal nature of the Malpighian tubules, is apparently not correct and has not received acceptance by other authors.

4. THE INVERSION OF CELL POLARITY IN THE EARLY GERM BAND (Text-fig. 2).

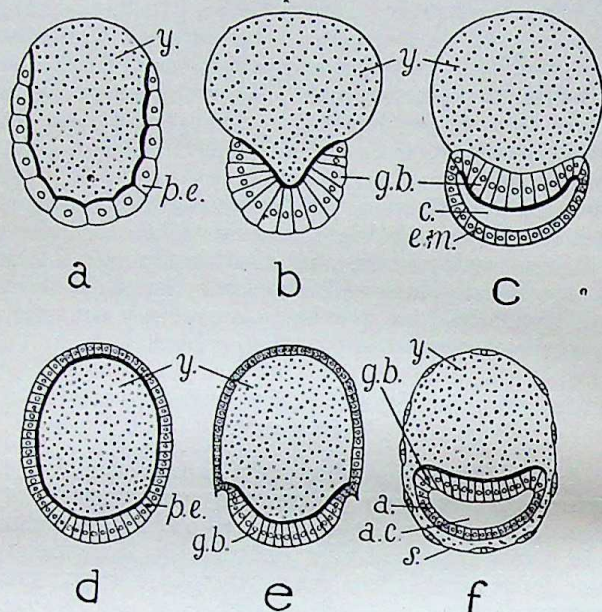
In 1903 BRUES described a peculiar condition in the Strepsipteran *Xenos peckii* where the yolk, instead of lying inside the vesicle formed by the primary epithelium comes to lie outside it. This condition was confirmed by HOFFMANN (1914) in *Xenos bohlsi*, and some years later by NOSKIEWICZ and POLUSZYNSKI (1928) in their careful work on *Stylops*. The latter authors further explained this condition by suggesting that there occurs, in the region of the germ band of the Strepsiptera, an inversion of cell polarity. As a result of the inversion, the inner or normally dorsal side of the cells, abutting in the beginning against the yolk, comes to point away from the latter and thus determines the ventral side of the future embryo. The outer ends of the cells, on the other hand, point towards the yolk and determine the dorsal side. In all other groups of insects, the inner walls of the cells determine the dorsal side of the future embryo, and the outer walls the ventral side.

5. THE SEGMENTATION OF THE HEAD (Text-fig. 3).

(a) Introductory.

The number of metameric segments composing the insect head has been variously estimated as from four to nine. An enumeration of all these views need not be made as they have been discussed recently by several authors, notably by WIESMANN (1926), EASTHAM (1930, b), LIMS (1937), SNODGRASS (1938) and WEBER (1938). It may, however, be mentioned that the number of segments most commonly regarded as entering into the head is either six or seven. The existence of the last five segments, viz., the antennary, the mandibular, the intercalary or

premandibular, the first maxillary and the second maxillary or labial, has been accepted by nearly all authors. HANSEN¹



Text-fig. 2 (a)-(f). Diagrams showing the inversion of cell polarity in the early germ bands of the Strepsiptera. Upper row (a)-(c)—*Xenos bohlsi* (HOFFMANN, 1914); lower row (d)-(f)—pterygote insect, other than the Strepsiptera, and in which both the amnion and the serosa are formed. The primary inner ends of the cells are shown in heavy line; the yolk is dotted. (a) and (d)—Early or primary epithelium stage. (b) and (e)—Later stage. In (b) the primary epithelium has shrunk, and the yolk is being extruded. In (e) the amniotic folds are being formed. (c) and (f)—Still later stage. In (c) the single embryonic membrane (=amnion plus serosa) is formed and the yolk is completely extruded. Note the inversion of cell polarity in the germ band, when compared to (f). In (f) both the amnion and the serosa have been formed. (After NOSKIEWICZ and POLUSZYNSKI, 1928.)

a., amnion; a.c., amniotic cavity; c., cavity between germ band and rudiment of embryonic membrane; e.m., rudiment of embryonic membrane (amnion plus serosa); g.b., germ band; p.e., primary epithelium; s., serosa; y., yolk.

(1893 and 1930) has claimed, on morphological grounds, the existence of a maxillular segment, as evidenced by the presence of a pair of reduced but true appendages, between the mandibles and the first maxillæ. The claim is supported by HENRIKSEN (1928). Recent work on apterygote embryology (SILVESTRI,

¹ HANSEN, H. J., 1893.—*Zool. Anz.*, vol. XVI, pp. 193-198 and 201-212.

— 1930.—*Studies on Arthropoda*. III.—Copenhagen.

1932), however, does not support this view, and the existing evidence for it must be regarded as inconclusive. The present discussion will, therefore, be confined to the segments lying in front of the antennary one. One or two of such segments have been variously claimed to exist, according as the total number of head segments is regarded as either six or seven, and have been known under a diversity of names, some of which are given below: (1) Head lobes segment or primitive head segment or protocephalic segment; its ganglionic constitution is homologous with the prostomial archicerebrum of the Annelida. (2) Ocellar segment. (3) Ocular segment. (4) Oral segment. (5) Acronic and preantennary segments. (6) Labral and encephalonic (brain) segments. Among the more important recent views concerning the segments lying in front of the antennary one, the following may be mentioned:—

WIESMANN (1926).—Two segments, the labral and the preantennary, exist. Acron is rudimentary and probably of no segmental importance. The head is regarded as 7-segmental.

EASTHAM (1930, b).—One segment, the labral, exists, and the protocerebrum is its ganglion. The preantennary segment is denied. The head is regarded as 6-segmental.

IMMS (1937).—Only one segment exists. The labrum does not represent a true segment. The first true segment is the preantennary or ocular. The head is regarded as 6-segmental.

HOLMGREN¹ (1916) and HANSTRÖM² (1927–1930).—The separation between the protocerebrum and deutocerebrum in insects and other Arthropoda is secondary, the two structures together being equivalent to the annelidan archicerebrum. The tritocerebrum is the neuromere of the first true segment, with the antennæ as its appendages. The labrum and the preantennary appendages belong to the category of prostomial tentacles of Annelids and are not true appendages. Behind the first or 'tritocerebral' segment come the three gnathal segments, the mandibular, maxillary and labial. The intercalary segment is denied. The head is regarded as 4-segmental. This view, which has been specially elaborated by HANSTRÖM, is accepted by SNODGRASS (1935), but has not gained wider support. It almost

¹ HOLMGREN, N., 1916.—*Kungl. Svenska Vetensk. Akad. Handl.*, vol. LVI, No. 1, pp. 1–303.

² HANSTRÖM, B., 1927.—*Zeit. f. Morph. Ökol. Tiere*, vol. VII, pp. 543–596.

——— 1928(a).—*Vergleichende Anatomie des Nervensystems der wirbellosen Tiere unter Berücksichtigung seiner Funktion.*—Berlin.

——— 1928(b).—*Zeit. f. Morph. Ökol. Tiere*, vol. XI, pp. 151–160.

——— 1929.—*Ibid.*, vol. XIII, pp. 329–358.

——— 1930.—*Ibid.*, vol. XIX, pp. 732–773.

completely disregards the evidence from embryology, such as the presence of appendages, cœlom sacs and neuromeres, and is for that reason unsound.

In a recent paper, SNODGRASS (1938) contends (p. 94) that 'a radial structure secondarily affects the anterior end of the articulate trunk because of the subapical position of the mouth'. Consequently, he argues, the cephalic cœlom sacs, being radial in position, cannot represent somites in the manner of paired sacs lying post-orally. The strong objection to this view is that cœlom sacs cannot lose their former segmental significance merely by virtue of their secondarily acquiring a radial position. In the same paper SNODGRASS suggests a new definition of the acron so as to represent by that term 'a primarily unsegmented archicephalon corresponding with the annelid prostomium' (p. 94). Such an acron, he contends, is represented in the arthropod embryo by the cephalic lobe (or lobes) bearing the eyes, the labrum, the preantennæ, and the first antennæ. It is difficult to accept this new definition until much stronger evidence than is hitherto available is forthcoming in favour of it. In the mean time it is desirable to retain the older definition of the acron as the unpaired apical portion of the arthropod head lying in front of the first true somite; such an acron is seen, among others, in *Scolopendra* (HEYMONS, 1901) and in *Carausius* (WIESMANN, 1926).

Before proceeding further, it needs to be pointed out that in appraising the segmental composition of the head, whilst evidence from morphology is obviously necessary, embryological evidence is still more important, as has been admitted by all but a few writers on the subject. In regard to the evidence from embryology, three criteria have been universally accepted as establishing the existence of a somite. These are the presence of (1) a pair of appendages; (2) a pair of cœlomic cavities; and (3) a neuromere, i.e., a pair of nerve ganglia homodynamous with the ganglia of the ventral nerve chain. Consequently, the recent discovery of a pair of preantennary appendages and of labral and preantennary cœlom sacs in some insects is of special interest. Its significance is discussed below, and, at the same time, a new interpretation of the segmental composition of the insectan protocerebrum is presented. Evidence from these sources, it may be added, points to a 7-segmental nature of the insectan head.

(b) *A New Interpretation of the Composition of the Insectan Protocerebrum.*

(i) *General.*

The insectan brain has hitherto been generally conceded as being composed of three primary portions, viz., the proto-, deuto- and tritocerebrum, corresponding to the first (labral,

preantennary, oral, ocular, etc.), second (antennary) and third (intercalary) cephalic segments. The view of HOLMGREN and of HANSTRÖM mentioned above, viz., that the proto- and deutocerebrum together form a single ganglionic unit equivalent to the prostomial archicerebrum of the Annelida, is unacceptable. The existence of the deutocerebrum as belonging to the antennary segment is well established on sound embryological grounds, and this as well as other cognate pieces of evidence are completely disregarded by these authors.

In the following account the deuto- and tritocerebrum are regarded, as heretofore, as discrete brain segments belonging to the antennary and intercalary somites respectively. With regard to the composition of the protocerebrum, however, a new interpretation is presented.

(ii) *The development of the protocerebrum.*

Each of the components of the brain, viz., the proto-, deuto- and tritocerebrum has been generally shown as developing from the ventral ectoderm in exactly the same manner as the other ganglia of the ventral nerve chain, and, therefore, as being homodynamous with the latter. While opinion is agreed that this is so in the case of the deuto- and tritocerebrum, the protocerebrum has long been regarded as developing in a more complicated manner and, therefore, possibly not being strictly homodynamous with the other two portions.

The embryological development of the protocerebrum has been best studied in the Orthoptera and the Dermaptera—by VIALLANES (1891) in *Mantis*; WHEELER (1893) in *Xiphidium*; HEYMONS (1895, a) in *Forficula*; and, more recently, by BADEN (1936) in *Melanoplus* and ROONWAL (1937) in *Locusta*. The observations of these authors agree in essential points and, for the following description, *Locusta* will be taken as an example. The protocerebral rudiments of *Locusta* lie on either side of the labrum and the stomodæal invagination and occupy the entire head lobes. They thus extend over a much more considerable area than either the deuto- or the tritocerebrum. From the very beginning, each half of the protocerebrum is divided into two lobes which are separated from each other by means of a hypodermal invagination. A third lobe, the optic lobe, is then differentiated from the lateral ectoderm in a manner different from and independent of the other two protocerebral lobes, but subsequently becomes connected with the latter. It is separated from the middle protocerebral lobe by means of a hypodermal invagination which, like the one between the other two lobes, disappears afterwards. In this manner, three protocerebral lobes are formed which are, following VIALLANES (1891), generally known as the first (optic), second and third lobes, counting from the outside. The number of rows of the primary or mother neuroblast cells is about 4-6 in the third lobe and about 3-4

in the second one. The development and fate of these neuroblasts is similar to those of the deuto- and tritocerebrum and of the ganglia of the ventral nerve chain (Table 1).

In the formation of the optic lobe, neuroblasts do not take part, and the lobe arises from the ectoderm at the dorso-lateral edge of the head lobes in the following manner:—The aforesaid region becomes thickened into a more or less rounded mass in which the peripheral nuclei are arranged in a single row, while in the rest of the mass they do not exhibit any regular arrangement. This mass is the common rudiment of the optic ganglion and the eye-plate. In a slightly older stage, the inner mass (the optic lobe) begins to cleft from the outer layer (the eye-plate), and sometime afterwards this separation is complete. In the mean time, the optic lobe becomes connected with the second protocerebral lobe which ultimately forms the opticon or internal medullary mass of the optic lobe and also the optic nerve. The optic lobe then gradually becomes differentiated into its various elements. During blastokinesis, the optic lobe acquires a connection with the eye-plate for the second time.

(iii) *The segmental significance of the composite nature of the protocerebrum* (Text-fig. 3 and Table 1).

The prevalent view is that the whole of the protocerebrum represents a single ganglionic pair homologous with the prostomial archicerebrum of the Annelida. WHEELER (1893) considered the possibility of the protocerebrum as being composed of more than one neuromere, but rejected it. WIESMANN (1926) remarked that, theoretically, the neuromeres of the labral and preantennary segments could be accepted as lying in the protocerebrum, but no proof was brought forward in support of the suggestion.

In the following discussion I have attempted to prove that the protocerebrum is composed of two neuromeres, the labral and the preantennary.

(α) *The optic lobes*.—The optic lobes (the so-called first protocerebral lobes) among insects develop either by invagination (Hymenoptera and Coleoptera) or by delamination (Orthoptera and Dermaptera). In neither case do neuroblasts share in their formation. A few doubtful cases of neuroblasts occurring in the optic lobes have been reported by VIALLANES (1891) in *Mantis* and by HEYMONS (1895, a) in *Forficula*, but, in view of the negative indications of all other authors, these exceptions need adequate confirmation before they can be accepted. If they are found to be correct, the neuroblasts in these instances would probably be regarded as having invaded the optic lobes secondarily. The entire manner, including the absence of neuroblasts, of the origin of the optic lobes in *Locustâ* and other insects clearly shows that they are not homodynamous with the other two lobes of the protocerebrum, nor are they

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TABLE I.

The ganglionic composition of the brain of Locusta, as compared to a ganglion of the ventral nerve chain.

Organ and its structure.	Brain.					A ganglion of ventral nerve chain.	
	Protocerebrum.			Deutocerebrum.	Tritocerebrum.		
	Two pairs of primary lobes (=two pairs of true ganglia).		One pair of secondary or optic lobes (the so-called first protocerebral lobes).				
	One pair of middle or second protocerebral lobes.	One pair of median (inner) or third protocerebral lobes.					
Ganglionic composition in relation to segment.	Labral ganglion (or first ganglion of head).	Preantennary ganglion (or second ganglion of head).	Not a true ganglion (and, therefore, of no segmental significance).		Antennary ganglion (or third ganglion of head).	Intercalary ganglion (or fourth ganglion of head).	Represents one body segment.
Number of primary neuroblasts taking part.	3-4	4-6	Nil.		4-5	4-5	

homologous with true segmental ganglia. Their connection with the rest of the brain is purely secondary and, therefore, in appraising the primary ganglionic constitution of the brain and the segmental composition of the head, they should be left entirely out of account.

(β) *The other two lobes.*—The second and third lobes may now be considered. Each of these lobes develops in a manner strictly homodynamous with a segmental ganglion of the ventral nerve chain. It is significant that the separation between the two lobes is noticeable from the very beginning of their appearance. As development proceeds, this separation becomes accentuated by the formation of an ectodermal inpushing in between the lobes. Moreover, whereas the number of rows of the primary or mother neuroblast cells sharing in the formation of each half of a ganglionic pair of the ventral nerve chain is 4 or rarely 5, double this number of rows of neuroblasts (about 8) is found in the two protocerebral lobes of each side taken together—4-6 in the third lobe and 3-4 in the second lobe. These facts suggest almost beyond doubt that each of the two protocerebral lobes, and not the whole of the protocerebrum, is homologous with a segmental ganglion of the ventral nerve chain. Consequently, the optic lobes being left out of account, the protocerebrum must be regarded as being primarily composed of two pairs of true ganglia, i.e., of two neuromeres. By virtue of their position, the median or inner pair of these ganglia (third pair of protocerebral lobes) is to be regarded as belonging to the second or preantennary segment of the head, and the middle or outer pair (second pair of protocerebral lobes) to the first or labral segment (Table 1).

(γ) *Comparison with Scolopendra.*—It is instructive to compare the structure of the insect brain, as interpreted above, with that of *Scolopendra* as elucidated by HEYMONS (1901). According to this author, the supraesophageal ganglion of *Scolopendra* is formed of the pro-, meso- and metacerebrum which are composed of the parts given below in Scheme 1.

I.—Front brain = Protocerebrum (*sensu lato*).

Procerebrum	Syncerebrum	1. Archicerebrum. (Unpaired.)
		2. Lamina dorsalis cerebri. (Paired.)
		3. Lobi frontalis. (Paired.)
		4. Lobi optici. (Paired.) (Not true ganglion.)
	Protocerebrum	5. Protocerebrum (<i>sensu stricto</i>). (Paired, and belonging to the preantennary segment.)

II.—Middle brain = Deutocerebrum.

Mesocerebrum	1. Lobi olfactorii seu antennales. (Paired and belonging to the antennary segment.)
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III.—Hind brain = Tritocerebrum.

Metacerebrum	1. Lobi tritocerebrales seu postantennales. (Paired and belonging to the intercalary segment.)
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Scheme 1.—The composition of the brain (supracæsophageal ganglion) of *Scolopendra*, according to HEYMONS (1901).

If we compare this condition with that of insects (e.g., *Locusta*; *Forficula*), a certain similarity becomes apparent. With regard to the homologies of the deuto- and tritocerebrum in the two groups, I am in agreement with HEYMONS (1901); but with regard to the homologies of the brain components lying anterior to these, I greatly differ (Table 2).

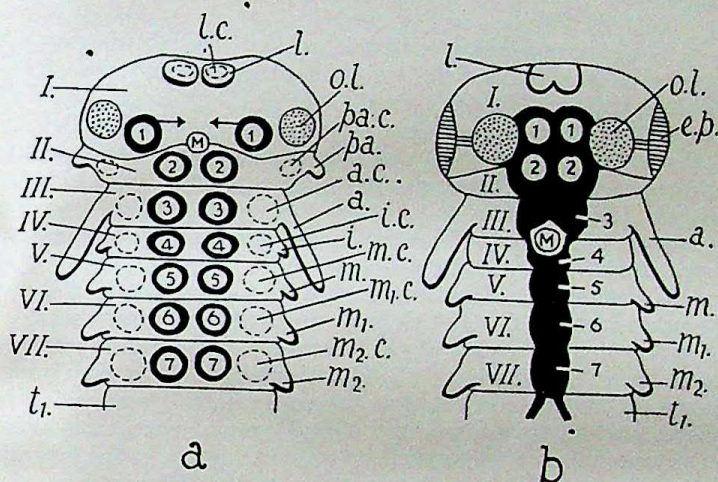
The unpaired anteriormost ganglion of the embryo of *Scolopendra* is regarded by HEYMONS as being represented by the anterior portion of the supracæsophageal commissure in insects. I disagree with this view. It would be more in consonance with the known facts if we were to believe that during the course of evolution the annelidan prostomium and its neurömere, the archicerebrum, undergo a progressive degeneration. Thus, in *Scolopendra* we still find a well marked 'archicerebrum' and the prostomium is reduced but clear as the 'acron'. In insects, reduction goes still further. The 'archicerebrum' completely disappears, but the prostomium is retained in some as the 'acron', although it disappears in most insects. It would be of extreme interest if a vestigial 'archicerebrum', somewhat akin to that of *Scolopendra*, were discovered in some

TABLE 2.
The homologies of the various components of the brain in the *Myriapoda* (Scolopendra) and the *Insecta*.

Brain of Insecta.		Brain of <i>Myriapoda</i> (Scolopendra)	
HEYMONS (1901).	ROONWÁL (present account).	HEYMONS (1901).	ROONWÁL (present account).
Composition.	Remarks.		
Disappears	These together form the insectan protocerebrum.	Anterior portion of the supra-oesophageal commissure.	
First protocerebral lobe or optic lobe. (Is not a true ganglion.)		First protocerebral lobe or optic lobe.	
Second protocerebral lobe or labral ganglion.		Second protocerebral lobe	
Third protocerebral lobe or preantennary ganglion.		Third protocerebral lobe	
Deutocerebrum		(Not yet demonstrated)	
Tritocerebrum		Deutocerebrum	
		Tritocerebrum	
		Archicerebrum (= prostomial archicerebrum of Annelida).	
		<i>Lobus opticus</i>	
		<i>Lobus frontalis</i>	
		<i>Lamina dorsalis cerebri</i>	
		Protocerebrum (<i>sensu stricto</i>)	
		Deutocerebrum	
		Tritocerebrum	

insect—it should be looked for in the Apterygota and the more primitive of the Pterygota.

The *lobus opticus* and the *lobus frontalis* of *Scolopendra* are regarded by HEYMONS as homologous with the first and second protocerebral lobes respectively of insects. During development, the *lobi opticus* and *frontalis* are intimately associated with each other, and HEYMONS himself remarks that the former probably arises in part from the latter. I am, therefore, inclined to regard both these *lobi* of *Scolopendra* as equivalent to the first protocerebral lobe (optic lobe) of insects which, as shown above, is not homodynamous with a true ganglion.



Text-fig. 3 (a)-(b). Theoretical diagrams of the anterior region of insect embryos, showing the 7-segmental nature of the insect head. Nerve ganglia are shown in heavy black, and coelom sacs in broken lines. The optic lobes are shown in stipple as they are not homodynamous with the nerve ganglia. (a) Early stage. All the coelom sacs and appendages of the head are seen. The nerve ganglia show their paired origin. The arrangement of the first two pairs of ganglia, viz., those of the labral and preantennary segments, differs from the rest. Arrows indicate the direction of subsequent migration of the first or labral pair of ganglia. (b) Later stage. The paired nature of the nerve ganglia is partly lost. The coelom sacs and the preantennary and intercalary appendages disappear. The oral aperture shifts backwards. The protocerebrum arises by the fusion of the first (labral) and second (preantennary) nerve ganglia and the optic lobes. The medial concentration of the appendages is not shown. (ORIGINAL.)

a., antenna; a.c., antennary coelom sac; e.p., eye-plate; i., intercalary or premandibular appendage; i.c., intercalary coelom sac; l., labrum; l.c., labral coelom sac; M., oral aperture; m., mandible; m₁, first maxilla; m₂, labium; m.c., mandibular coelom sac; m₁c., first maxillary coelom sac; m₂c., labial coelom sac; o.l., optic lobe; pa., preantenna; pa.c., preantennary coelom sac; t₁, first thoracic segment; 1-7, first to seventh nerve ganglia of head, thus: 1, labral; 2, preantennary; 3, antennary; 4, intercalary; 5, mandibular; 6, first maxillary; and 7, labial; I.-VII., first to seventh head segments.

The *lamina dorsalis cerebri* of *Scolopendra* is homologized by HEYMONS with the third protocerebral lobe of insects whereas, by its position, it should, in my opinion, be homologized with the second protocerebral lobe (which is the neuromere of the labral segment).

The 'protocerebrum' (*sensu stricto*) of *Scolopendra* has, according to HEYMONS, not been demonstrated in insects, but I would suggest its homologue in the third protocerebral lobe of insects which was first demonstrated long ago by VIALLANES (1891).

(c) *The Labral Segment.*

(i) *The appendages.*

I shall discuss below whether or not the labrum can be regarded as representing the true and paired appendages of the labral segment. Morphologically, the labrum is not an unimportant structure. This is suggested by its wide distribution in the Insecta, Myriapoda and Crustacea, and it is certainly homologous in these three groups. The characters by which we recognize structures as being truly segmental appendages are (i) that they should arise in ontogeny as paired, hollow ectodermal evaginations; and (ii) that each member of the pair should possess a coelom sac, a portion of which is primarily lodged inside the appendage itself. On this basis, the following points support the appendicular nature of the labrum: (1) Its rudiments are paired in several insects. (2) The occurrence, in a number of insects, of an independent *pair* of coelom sacs lying inside the labrum. The newly discovered labral coelom sacs are of great importance in establishing the appendicular nature of the labrum. They bear precisely the same relation to the labrum as do the other coelomic cavities to their respective appendages. To disregard this evidence would involve the assumption of three independent postulates (ROONWAL, 1937) as follows:—(a) That the close association between the labral pair of coelom sacs and the labrum is purely accidental and of no morphological significance. (b) That the labral coelom was originally unpaired in conformity with the unpaired labrum and that its paired nature is secondary. (c) That the very existence of the labral coelom, whether paired or (theoretically) unpaired, is a secondary phenomenon. All the three postulates appear to be highly improbable.

The following points are generally put forth as disproving the appendicular nature of the labrum, but as will be shown below, and as has been recognized by several other authors, all these objections are without sound foundation:—

1. The labral rudiments, in contrast to those of the other body appendages arise medianally to the neural swellings.—It is now recognized that all the cephalic appendages, particularly those lying towards the anterior and posterior extremities of

the head, undergo, during ontogeny, a concentration towards the median line (ROONWAL, 1939, a). The labrum, like its counterpart at the other extremity of the head, the labium, comes to lie on the median line itself, with this difference that while the medial concentration of the labium occurs in ontogeny, that of the labrum may be said to occur, to a very considerable extent, in phylogeny, so that already in the early embryo its paired rudiments arise close to the median line. In some insects this concentration takes place so early in phylogeny that the labrum arises, from the beginning, as an unpaired rudiment in the middle line.

2. The labrum, unlike the other true appendages, is never segmented.—This character is shared by the preantennary, intercalary and several abdominal appendages, all of which are admitted as truly appendicular. Moreover, some of the abdominal appendages, such as those which form the uropods and cerci, even though they persist like the labrum in the adult insect, do not undergo any segmentation.

3. The labrum, unlike the other cephalic appendages, occupies a pre-oral position.—The antennæ of the Onychophora are also pre-oral, and yet are correctly regarded as true segmental appendages (WIESMANN, 1926, p. 154).

It would thus appear that the balance of evidence is in favour of the appendicular nature of the labrum, and this view is accepted here.

(ii) *The coelomic cavities.*

The occurrence of a pair of coelomic cavities in close association with the labrum has been recently demonstrated in *Carausius* (WIESMANN, 1926), *Rhodinus* (MELLANBY, 1936) and *Locusta* (ROONWAL, 1937).¹ That these are true and independent coelomic cavities, there appears to be no doubt. Like the other coelomic cavities, they are bounded by a layer of mesodermal cells and lie in the hollow of their appendage, the labrum. The only way in which they differ from the others is in their comparatively small size, but this difference cannot obviously be of much significance. The objection of MANTON (1928, p. 455) that the labral coelom sacs of *Carausius* may represent the original aorta-forming part of the preantennary somite cannot be maintained. She lays stress on the connection between the labral and preantennary coelom sacs *via* the stomodæal mesoderm. Such connections, by means of solid mesodermal strands, occur in several other head and trunk segments both in *Carausius* and *Locusta*, and are probably of little significance. Moreover, in *Locusta*, while the labral coelomic cavities are present, there is no trace of the preantennary coelom, and this condition shows that the former should be considered not as derivatives of the latter, but rather as independent structures. Again, in *Locusta*

¹ Also in the stone-fly *Pteronarcys* by MILLER (1939), see Appendix, p. 105.

the mesoderm of the labral coelom sacs of each side is quite independent and is unconnected either with its fellow of the other side, or with the stomodæal mesoderm, or the mesoderm of any other segment.

While clear hollow labral coelom sacs have been demonstrated in only a few insects, paired mesodermal masses, developing in association with the labrum and indicative of collapsed or disorganized coelom sacs, have been shown in several insects as follows:—In *Forficula* by HEYMONS (1895, *a*); in *Chalicodoma* by CARRIÈRE and BÜRGER (1897); in some other Hymenoptera by STRINDBERG (1914, *a*); and in *Pieris* by EASTHAM (1930, *b*). In *Forficula* these masses are distinctly bi-layered and there can be little doubt of their being homologous with coelom sacs. Thus it will be seen that the existence of either the labral coelom sacs or the paired labral mesoderm masses clearly indicative of their coelom-sac origin have been found in insects belonging to at least six different orders, viz., Orthoptera, Dermaptera, Hymenoptera, Lepidoptera, Plecoptera and Hemiptera. It is perhaps significant that they are best developed in more primitive orders like the Orthoptera and the Hemiptera and less so in the more specialized orders. For the same reason, the fact that they are ill-developed or absent in orders like the Diptera and the Coleoptera is only to be expected since several of the other coelom sacs are also suppressed here. They have not so far been demonstrated in the Apterygota.

(iii) *The neuromere.*

It has been shown above that, developmentally, the protocerebrum must be regarded as consisting of *two* neuromeres, viz., the second and third protocerebral lobes. Of these, the second lobe is the labral neuromere and the third lobe the preantennary neuromere (Text-fig. 3). This demonstration completes the evidence in favour of the existence of the labral segment.

It must, however, be pointed out that in post-embryonic life the labrum is innervated from the tritocerebrum and not from the median protocerebral lobes. The existence of this condition would appear to be a serious obstacle in accepting the above view, were it not for the fact that the tritocerebral innervation of the labrum is in all probability a secondary feature in so far as the relation of the neuromere and its segment is concerned. The tritocerebrum belongs, without doubt, to the intercalary and not to the labral segment. As to why the labrum should be innervated not by its own neuromere but by one lying three segments behind it, yet remains to be shown.

(d) *The Preantennary Segment.*

WIESMANN (1926) in *Carausius* has been the first, and so far the only, author to demonstrate the existence of a

rudimentary pair of preantennary appendages and coelom sacs. Both these characters support the existence of a preantennary segment. The recognition of the third protocerebral lobe as the preantennary ganglion (Text-fig. 3) has been mentioned above.

(e) *Conclusions.*

It has been shown above that, on embryological criteria, we must accept the existence of both the labral and the preantennary segments in insects. These, together with the five following segments, viz., the antennary, intercalary, mandibular, first maxillary and labial, would indicate a 7-segmental nature of the insect head (Table 3).

The chief difficulty in accepting two segments in front of the antennary one is that the scheme does not easily fit in with the condition regarded as occurring in other Arthropods, particularly other Mandibulata, for two pairs of coelom sacs and of neuromeres lying in front of the somite of the second antennæ have not so far been demonstrated in them. Indications of the existence of either the one or the other of these two segments are, however, evident. Thus, the preantennary coelomic cavities of insects (*Carausius*) obviously have their homologue in the cavities bearing a similar name in the Chilopod *Scolopendra* (HEYMONS, 1901); in the precheliceral somite of spiders (KISHINOUE, 1894) and *Scorpio* (BRAUER, 1895); and finally, in the newly discovered preantennular coelomic cavities of the Mysid Crustaceans, *Hemimysis* (MANTON, 1928) and *Mesopodopsis* (NAIR, 1939), and the similar but solid somites of *Nebalia* (MANTON, 1934). Labral coelom sacs have not yet been found in these instances. Appendages of the 'preantennary' segment have so far been demonstrated only in the Insecta and Chilopoda, but not in the Crustacea and Arachnida.

On the other hand, the coelomic cavities claimed by PFLUGFELDER (1932) to occur in the clypeus of the Diplopod *Platyrrhacus* would, by virtue of their position in the clypeus, seem to correspond to the labral rather than to the preantennary coelomic cavities of insects, although PFLUGFELDER inclines to the latter possibility. A second pair of pre-oral coelomic cavities does not occur in *Platyrrhacus*. As in insects, the labrum could be regarded as the appendage of the first segment.

Regarding the neuromeres, it has been shown above that in *Scolopendra* the *lobi opticus* and *frontalis* together represent the first protocerebral lobe (optic lobe) of insects and do not, therefore, constitute a true ganglion. These, together with the 'archicerebrum', the labral neuromere or *lamina dorsalis cerebri* and the preantennary neuromere or 'protocerebrum *sensu stricto*', of HEYMONS, form the protocerebrum *sensu lato* which is homologous with the entire insectan protocerebrum. Thus, for Chilopods at least, the evidence in favour of the existence of two

TABLE 3.

Showing the 7-segmental plan of head segmentation in

Nature of segments.	Segment number.	INSECT	
		Segment.	Neuromere.
Primary head segments (procephalonic).	1	Labral ¹ (WIESMANN, 1926; MELLANBY, 1936; ROONWAL, 1937; MILLER, 1939). ²	Labral ganglion. [Middle protocerebral lobe. (Second lobe of VIALLANES, 1891.)]
	2	Preantennary ¹ (WIESMANN, 1926).	Preantennary ganglion. [Inner protocerebral lobe. (Third lobe of VIALLANES, 1891.)]
	3	Antennary	Deutocerebrum ..
	4	Intercalary (premandibular or postantennary).	Tritocerebrum ..
Secondary head segments (gnathocephalonic).	5	Mandibular	Mandibular ganglion ..
	6	Maxillary	Maxillary ganglion ..
	7	Labial	Labial ganglion ..

¹ Authors who have demonstrated the coelom sacs² See Appendix, p. 105.

TABLE 3.

the Insecta (cf. Chilopoda, Diplopoda and Crustacea).

Cœlom anes.	Appendages.	CHILOPODA (<i>Scolopendra</i>). (Segments).	DIPLOPODA (<i>Platyrrhacus</i>). (Segments).	CRUSTACEA. (Segments).
Present	Labrum	Labral (?)	Labral ¹ (PFLUGFELDER, 1932)	Labral (?).
Present	Preantennæ. (Are rudimentary and evanescent).	Preantennary ¹ (HEYMONS, 1901).	Preantennary (?)	Preanten- nulary ¹ (MANTON, 1928; NAIR, 1939).
Present	Antennæ	Antennary	Antennary	Antennulary (first antennary).
Present	Intercalary (pre- mandibular) appen- dages or post- antennæ. (Are rudimentary and evanescent).	Intercalary (pre- mandibular).	Intercalary. (Not present in <i>Platyrrhacus</i> , but found in some other Diplo- pods).	Antennary (second antennary).
Present	Mandibles	Mandibular	Mandibular	Mandibular.
Present	Maxillæ	First maxillary	First maxillary	First maxillary.
Present	Labium	Second maxillary	Second maxillary	Second maxillary.

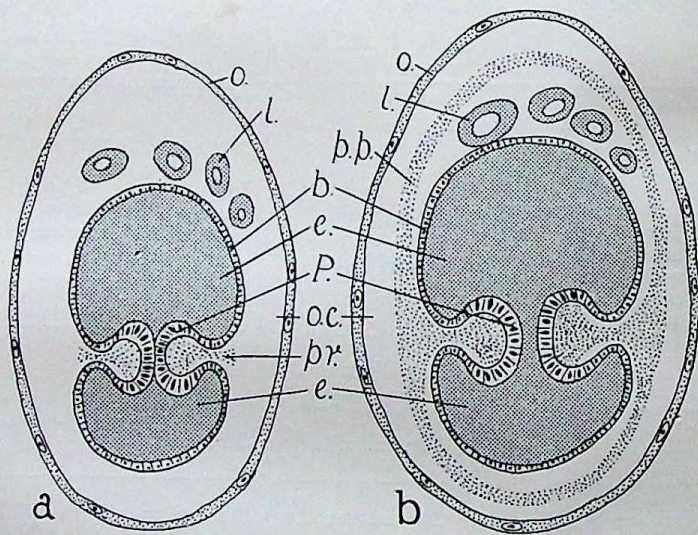
of these segments are given within brackets.

segments lying in front of the antennary one, and thus of a 7-segmental head, is fairly conclusive, with this difference that labial cœlom sacs have not yet been demonstrated. The same, however, cannot be said for the Diplopoda and the Crustacea.

6. THE PLEUROPODIA.

Insect pleuropodia or appendages of the first abdominal segment have a problematic function, variously conjectured as respiratory, secretory and excretory, etc. Recently, however, some information has been forthcoming regarding their function, and it would appear that they may perform variable functions in different insects.

HAGAN (1931) has shown that in *Hesperoctenes fumarius* Westwood, a viviparous Hemipteran belonging to the family Polyctenidæ, the pleuropodia serve as a pseudo-placental organ of the embryo (Text-fig. 4). Several embryos lie freely, as a



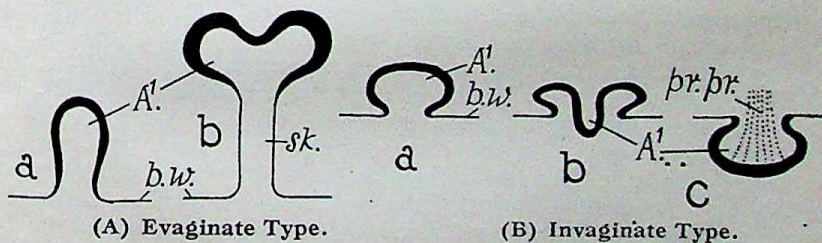
Text-fig. 4 (a)-(b). Two stages in the development of the pleuropodial pseudo-placenta in *Hesperoctenes fumarius*. Diagrammatic. (a) Stage of invaginated pleuropodia which touch each other medially. Note the protoplasmic processes. (b) Stage with the completed pleuropodial pseudo-placenta. (Based on and greatly modified from HAGAN, 1931.)

b., body-wall of embryo; e., embryo; l., legs; o., wall of maternal genital duct; o.c., cavity of maternal genital duct; P., pleuropodium; p.p., pleuropodial pseudo-placenta; pr., protoplasmic processes of pleuropodium.

rule, in the maternal reproductive tracts and the eggs are devoid of yolk. The pleuropodia arise like normal limb-bud evaginations, but shortly before blastokinesis they become invaginated

into the body until the pleuropodia of the two sides touch each other. After blastokinesis, the invaginated pleuropodial cells send out long protoplasmic processes which ultimately surround the embryo completely on the outside and thus form a pseudo-placental organ. Unlike the pseudo-placental organ of the Dermapteran *Hemimerus talpoides* (HEYMONS, 1912) and of the Psocopteran *Archipsocus fernandi* (FERNANDO, 1934), that of *Hesperoctenes* is not directly attached to the maternal body, and the embryo lies quite freely. HAGAN suggests that it absorbs the nutritive fluids from the genital ducts and transports them to the embryo. (Also see p. 53; and Appendix, p. 105.)

Recently, SLIFER (1937) has claimed that the pleuropodia of the grasshopper *Melanoplus differentialis* are the seat of a hatching enzyme which serves to dissolve the tougher portions of the egg-coverings and thus facilitates hatching. The evidence brought forth by her in support of the claim is, however, indirect. By ligaturing the egg above or below the pleuropodia, SLIFER claims to have shown that one of the egg-coverings, viz., the 'white cuticle', is dissolved only in the portion containing the pleuropodia, but remains unaffected in the other half of the egg. When the pleuropodia are removed from the embryo, the 'white cuticle' remains more or less undissolved. From this, she concludes that the pleuropodia secrete a hatching enzyme. While SLIFER's experiments are suggestive, more work is obviously needed before her claim can be substantiated, especially in view of the fact that the pleuropodia have been shown to undergo, in some other Acridids, viz., *Stenobothrus* (GRABER, 1888, a; 1889, b) and *Locusta* (ROONWAL, 1937), a progressive degeneration after blastokinesis until, at the time of hatching, they are reduced to partially cuticularized, shrivelled up masses, apparently of no physiological significance. More recently, SLIFER (1938, b) has brought forward some cytological evidence in support of her contention.



Text-fig. 5 (A)-(B). Diagrammatic representation of the two main types of development of insect pleuropodia. (A)—Evaginate Type. (B)—Invaginate Type. (a), (b), (c)—Various consecutive stages of development. (After ROONWAL, 1937.)

A¹, pleuropodium; b.w., body-wall of germ band; pr. pr., protoplasmic processes of pleuropodium.

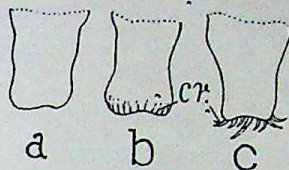
Although a considerable mass of data regarding the development of the pleuropodia exists (*vide* HUSSEY, 1926), no serious attempts had, until lately, been made to classify their various modes of development. Recently, however, ROONWAL (1937) has classified insect pleuropodia into two types: (i) *Evaginate type*, when they remain evaginate throughout their developmental history. Their distal end may undergo a slight invagination, but the latter does not sink beneath the body wall of the embryo. (ii) *Invaginate type*, when they invaginate into the body before finally disappearing (Text-fig. 5).

7. THE OTHER ABDOMINAL APPENDAGES.

While the existence of embryonic abdominal appendages, homodynamous with the thoracic legs, has been recorded in most insects, opinion has been somewhat divided firstly, as to their appendicular nature and secondly, as to whether they persist in post-embryonic life, and if so, in what form. The eighth to eleventh abdominal appendages are usually retained as gonapophyses, cerci, etc., while the first seven appendages have generally been regarded as completely disappearing except in the Apterygota where a variable number of them is retained in the adult stage. HAASE (1889, a) conjectured that in *Machilis* and *Blatella* (*Blatta*, *Phyllodromia*) some of the anterior abdominal appendages take some share in the formation of the lateral parts (pleuron?) of the ventral plate and this view was supported by GRABER (1889, c; 1890) in *Melolontha*. Modern research has not lent support to this view, but the point deserves careful reinvestigation especially in view of the fact that the thoracic pleura, as will be shown below (p. 56), have been definitely demonstrated to be derived from their respective limb base or subcoxa.

Regarding the prolegs of the carterpillars (Lepidoptera) and of the carterpillar-like larvæ of the saw-flies (Tenthredinidae), KOWALEWSKY (1871), TICHOMIROFF (1882) and GRABER (1890) in *Bombyx* and *Hylotoma*, derived them directly from true abdominal appendages. This view, however, was opposed by others who regarded the prolegs as secondary formations first developed in the larva. KORSCHULT and HEIDER (1892), reconciling these two views, suggested that the embryonic abdominal legs, although disappearing from view, are not completely lost: their vestiges remain latent for a time and later become reactivated in the larva to form the prolegs. The recent work of FRIEDMANN (1934) is, therefore, of interest in finally deciding this point, at least for the Lepidoptera. She has shown that the prolegs of *Chærocampa elpenor* and *Odonestis potatoria* are directly derived from the embryonic abdominal appendages and should, consequently, be regarded as truly appendicular structures (Text-fig. 6). She has seen these transformations in abdominal segments 3-6 and 10. EASTHAM

(1930, b) found a similar condition in *Pieris rapæ*. The nature of the abdominal feet of the larvæ of the saw-flies has not



Text-fig. 6 (a)-(c). Development of the prolegs or abdominal feet of *Odonestis potatoria*. (a)—Abdominal appendage of 8½ days old embryo. (b)—Same of 9½ days old embryo. The rudiments of the crochets are being laid. (c)—Same of 10½ days old (nearly fully developed) embryo. The crochets are complete. (Adapted from FRIEDMANN, 1934.)

cr., chrochets.

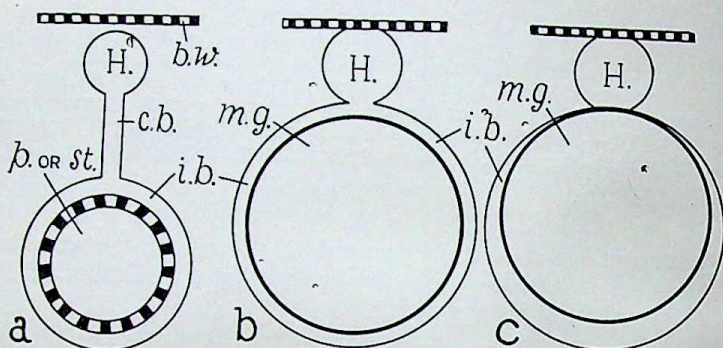
yet been studied, but it is probable that these structures will be found, as in the Lepidoptera, to be direct derivatives of the embryonic abdominal appendages.

8. THE EMBRYONIC BLOOD SINUSES.

The existence of numerous transient embryonic blood sinuses in insects is of considerable phylogenetic interest when we recall that these sinuses, along with the heart, represent the primitive body cavity or schizocoel of the Annelids, and not the secondary body cavity or coelom. The definitive body cavity of insects is a hæmocoel which almost completely replaces the coelom. Of the schizocoelic sinuses in insects, the circum-intestinal blood sinus is of special importance as it is undoubtedly homologous with a similar structure in the Annelids where it is connected with the heart throughout life by means of a long connecting sinus. The various stages by which this connection becomes severed in insects, so that ultimately the circum-intestinal blood sinus remains only as an embryonic organ of recapitulatory and not functional interest, have been recognized by HIRSCHLER (1924) and by ROONWAL (1937). So far, the following three stages have been discovered (Text-fig. 7):—

- (a) The heart opens into the circum-intestinal blood sinus by means of a long connecting sinus. This condition is found in the distal proctodæal region of *Donacia* (HIRSCHLER, 1909, a), and in the distal mesothoracic region of *Locusta* (ROONWAL, 1937).
- (b) The heart directly opens into the circum-intestinal blood sinus without the intervention of a connecting sinus. This condition occurs in *Carausius* (WIESMANN, 1926).

(c) The heart does not open into the circum-intestinal blood sinus, but merely abuts on the mid-dorsal wall of the latter. This condition occurs in *Locusta* (ROONWAL, 1937) throughout the length of the heart, except in the distal meso-thoracic region where the condition described above in (a) obtains.



Text-fig. 7 (a)-(c). Stages in the evolution of the relation between the circum-intestinal blood sinus and the heart in insects. (a)—Proctodæal region of *Donacia* or distal mesothoracic region of *Locusta*. (b)—Mid-gut region of *Carausius*. (c)—Mid-gut region of *Locusta*. (After ROONWAL, 1937.)

b.w., dorsal body-wall of embryo; c.b., connecting sinus between heart and circum-intestinal blood sinus; H., heart; i.b., circum-intestinal blood sinus; m.g., mid-gut; p., proctodæum; st., stomodæum.

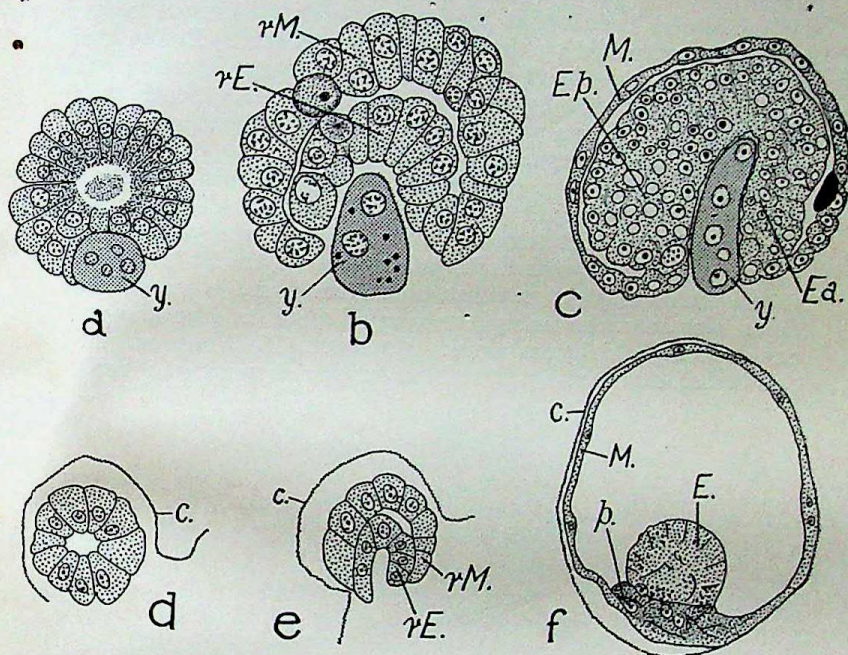
9. POLYEMBRYONY AND THE EMBRYONIC MEMBRANES.

Recent advances in the field of polyembryony and the origin and fate of the embryonic membranes in polyembryonic insects have been summarized by IMMS (1937), and I need not, therefore, go into the subject here.

The persistence of a small portion of the serosa in *Locusta* (ROONWAL, 1935, b; 1937) may be mentioned. In this insect, while the greater portion of the serosa degenerates by the formation of a dorsal organ, a small portion of it at the extreme posterior (micropylar) end of the egg remains unaffected. The *posterior serosal patch*, as this structure has been termed, actually undergoes further development by becoming bi-layered and thus developing a cavity. This arrangement persists until hatching when the posterior serosal patch is cast off with the egg-shell. In no other insect has such a structure been described and its significance is as yet obscure.

NOSKIEWICZ and POLUSZYNSKI (1928) have shown that in *Stylops* (Strepsiptera) there is formed only one embryonic membrane which they regard as equivalent to the amnion plus

serosa of other insects. It may be mentioned that this condition strongly recalls the one described long ago by SCLATER (1888) in *Peripatus imthurni* (Onychophora) in his so-called pseudo-gastrula¹, with this difference that unlike as in *Stylops*, the embryonic 'cup' of *Peripatus* does not hold any yolk in its hollow (Text-fig. 8) (also see p. 27). As pointed out by KORSCHULT



Text-fig. 8 (a)-(f). Figures showing the formation of the embryonic membrane.

(a)-(c)—*Stylops* sp. (The figures have been turned upside down for facility of comparison with *Peripatus*.) Note the extruded yolk mass.

(a)—Blastula-like stage. (b)—The cup-like stage, showing the differentiation of the germ band proper and the embryonic membrane. (c)—Later stage. (Adapted from NOSKIEWICZ and POLUSZYNSKI, 1928.)

(d)-(f)—*Peripatus imthurni*. (d)—Blastula-like stage. (e)—The cup-like stage (pseudo-gastrula of SCLATER) showing the differentiation between the embryo proper and the embryonic membrane. (f)—Later stage. (After SCLATER, 1888.)

c., cuticular (?) membrane bounding the maternal uterus internally; E., embryo proper; Ea., anterior end of embryo; Ep., posterior end of embryo; M., embryonic membrane; p., placenta-like growth of cells; rE., rudiment of embryo; rM., rudiment of embryonic membrane; y., extruded yolk mass.

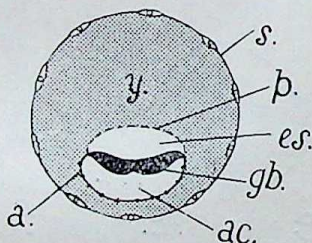
¹ KENNEL (1885; 1888) interpreted a similar condition in *Peripatus edwardsii* in an entirely different way which is probably wrong. He regarded the outer membrane of SCLATER as a derivative of the maternal uterine epithelium. WILLEY's (1898) observations on *Peripatus novae-britanniae* would appear to support SCLATER's view.

and HEIDER (1899), the single embryonic membrane of *Peripatus imthurni* might supply a clue to the origin of the double embryonic membranes, the amnion and the serosa, of insects. The condition in *Stylops* strongly supports this suggestion.

10. THE PROVISIONAL DORSAL CLOSURE OF THE EMBRYO.

It is well known that the definitive dorsal closure of the embryo is completed by the germ band ectoderm. Before this, however, the majority of insect embryos undergo a provisional dorsal closure formed by the amnion, the serosa, or both these membranes. This provisional dorsal closure is then replaced by the germ band ectoderm.

In the Acrididae a remarkable type of provisional dorsal closure has been found. GRABER (1888, a) first discovered in *Stenobothrus variabilis* that the lateral edges of the young germ band give rise, at a point slightly above the origin of the amnion, to an ectodermal outgrowth which soon forms a provisional dorsal closure of the embryo, cutting off the latter from the yolk and enclosing an epineural sinus. ROONWAL (1937) has confirmed this in *Locusta* (Text-fig. 9) and has further shown that it repre-



Text-fig. 9. Diagrammatic representation of a transverse section of the early embryo of *Locusta*, showing the early or first provisional dorsal closure. (Based on ROONWAL, 1937.)

a., amnion; ac., amniotic cavity; es., epineural sinus; gb., germ band; p., provisional dorsal closure; s., serosa; y., yolk.

sents only the first provisional dorsal closure, and is followed by others. The fate of the first provisional dorsal closure of *Locusta* is remarkable. At first it serves as a gliding surface beneath which the splanchnic mesoderm progresses medianally. After some time the splanchnic mesoderm separates from the first provisional dorsal closure at the lateral edges of the germ band, and in this way the first pair of lateral embryonic blood sinuses are formed. The blind ends of the stomodæum and the proctodæum are also closely attached to the first provisional dorsal closure. During blastokinesis the portion of the first provisional dorsal closure lying between the blind ends of the stomodæum and the proctodæum snaps at the edges and grows round the yolk in the same way as the amnion lying dorsal to the embryo

and the portion of the serosa lying anterior to the latter. Its pre-stomodæal and post-proctodæal portions remain unchanged until sometime after blastokinesis when they probably degenerate, being replaced by the definitive dorsal closure formed by the hypodermis. Mid-dorsally, the first provisional dorsal closure is fused with the amnion, the latter forming the *second or amniotic provisional dorsal closure* of the embryo. The first provisional dorsal closure at this stage forms the *first provisional mid-gut epithelium*. Afterwards, the splanchnic mesoderm grows round the yolk and separates the first provisional dorsal closure from the amnion. The first provisional dorsal closure then degenerates, leaving the inner layer of the splanchnic mesoderm as the *second provisional mid-gut epithelium* until the definitive mid-gut epithelium is formed from the 'end-ectodermal masses', as has been mentioned above. The second or amniotic provisional dorsal closure of the embryo is soon replaced by the *definitive dorsal closure* formed by the extension of the lateral ectoderm. Thus, two provisional dorsal closures are formed in some insects, the first one of these being peculiar to the Acrididæ.

11. BLASTOKINESIS.

(a) Mechanism of Blastokinesis.

Some precise knowledge has accumulated recently regarding the mechanism of blastokinesis. SLIFER (1932, a), THOMPSON (1934) and ROONWAL (1937) have observed it in the living eggs of representatives of the family Acrididæ. In *Locusta* (ROONWAL), about two to three hours (at 33°C.) before the beginning of blastokinesis, peristaltic movements originating at the caudal and proceeding towards the cephalic end of the embryo are seen. At the same time, the entire embryo pulsates in such a way that its dorsal surface abutting on the yolk expands and contracts. Each pulsation lasts for about 1 to 2 seconds, with intervals of 3 to 6 seconds between succeeding pulsations. The peristaltic movements cause the head of the embryo to strike against the embryonic membranes and rupture them. The latter contract on rupturing and the embryo now turns round the posterior pole of the egg and reaches its dorsal surface. SLIFER found also that in *Melanoplus femur-rubrum* the embryo after completing revolution 'turns slowly on its long axis until its ventral portions lie beneath the concave surface of the egg'. In *Locusta* blastokinesis takes, when it proceeds smoothly, about 17-20 hours for its completion at 33°C. Sometimes, however, it stops for several hours at various stages of the process and may take nearly double the above time. In *Melanoplus* SLIFER found that blastokinesis may be partially gone through even though the serosa remains unruptured. She also found that, in exceptional

cases when blastokinesis fails to occur, development may continue inspite of this defect and a normal animal result.

THOMPSON (1934) has made a detailed study of the rhythmic contractions of the lateral body walls of the embryo of *Melanoplus femur-rubrum*. The contractions commence during blastokinesis and are synchronous with the heart-beats when the latter make their appearance. These activities fall into three chronological periods: (i) From blastokinesis to yolk engulfment, in which the movements are slow, being of the order 15-20 per minute at 25°C., are at times irregular and may even exhibit reversibility in the direction of movement. (ii) From yolk engulfment to nearly the moment of hatching, in which the rate of the contractions increases rapidly to 120-150 per minute. (iii) A period during which this high rate of contraction is maintained at a fairly constant level.

(b) Theories of Blastokinesis.

Little exact knowledge exists regarding the physiological significance of blastokinesis, but a number of theories have been put forth and are briefly described below:—

1. *Illusion theory*.—Some of the earlier authors believed that blastokinesis is not an active process but an illusion caused by the development of the various body parts in such a way that the embryo seems to undergo a change of position. In view of the fact that vigorous movements of the embryo take place during and just before blastokinesis, and that the revolution of the embryo has now been established beyond doubt, this theory has no foundation.

2. *Chemical theory*.—WHEELER (1893) suggested that the embryo turns in order to get away from the waste products of metabolism and to go to a 'healthy' territory of the yolk. The objections to this view are (i) that waste products can diffuse throughout the egg, and (ii) that several insects undergo no blastokinesis.

3. *Spatio-mechanical theory*.—TIRELLI (1931, a) suggested that the silk-worm embryo turns in order to give more space to the dorsal side. In the pre-blastokinetic period, the ventral side of the embryo is convex and, therefore, provides a greater space for the development of the organs than the dorsal side which remains comparatively undeveloped for a long time. At a critical stage, when the development of the ventral side is more or less complete, the embryo turns round so as to give more space to the dorsal side which then becomes convex. This hypothesis has been accepted by GRANDORI (1932, a).

It must, however, be admitted that we are still far from fully understanding the true significance of blastokinesis.

12. VIVIPARITY.

Various types of viviparity had been known in insects since a long time, but no satisfactory classification of these types existed. The classification recently proposed by HAGAN (1931), therefore, serves a very useful purpose. Four types of viviparity, depending largely on the nutritive arrangements of the embryo, have been recognized by HAGAN, and the last type has been further subdivided here into a number of classes. The various types are described below :—

1. *Ovo-viviparity*.—The egg contains a sufficient amount of yolk to nourish the embryo until hatching. The larva, until it is extruded by the mother, does not receive additional nutriment from specialized organs. Examples: Some Coccidæ; some Coleoptera; Sarcophagidæ; the Psocopteran, *Hyperetes guestphalicus* (JENTSCH, 1936); and others.

2. *Intussuctio-viviparity*.—The egg contains a sufficient amount of yolk to nourish the embryo until hatching. The larva is retained in the maternal uterus and is nourished by means of secretions from specialized organs, such as uterine glands, of the mother. No placenta-like organs are formed. Examples: *Glossina*; some Muscidæ; and the Pupipara.

3. *Exogenito-viviparity*.—The egg contains little or no yolk. The embryo, in a stage of development corresponding to the egg stage of the ovo-viviparous forms, obtains its nourishment directly from the maternal tissues by means of a trophamnion, trophserosa, or trophchorion. Development occurs in the maternal hæmocoel and not in the genital tract. Examples: Strepsiptera.

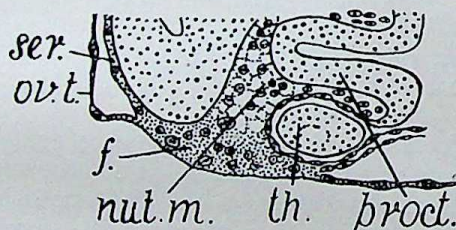
4. *Pseudoplacento-viviparity*.—The egg contains little or no yolk. The embryo develops in the genital ducts of the mother and receives from the latter, at least for some time, a supply of nutriment by means of a placenta-like organ called the pseudo-placenta. Examples: *Hesperoctenes* (Hemiptera); *Hemimerus* (Dermaptera); *Archipsocus* (Psocoptera); and others. Under this head, I propose the following further sub-types:—

(a) *Attached embryo type*.—In this case the embryo is attached by means of the pseudo-placenta to the maternal body for a varying period. This is further divisible into the following three types depending on the origin of the pseudo-placenta which may arise as follows:

(i) *Exclusively from the maternal tissues*.—In the parthenogenetic eggs of viviparous aphids, WILL (1888) showed that after the development of the 'blastoderm', the egg contains only a small amount of food-yolk—the

so-called 'primary food yolk'—in which a few yolk cells are found. This yolk soon disappears. Subsequently, however, the embryo is provided by a fresh mass of yolk—the so-called 'secondary yolk or pseudo-vitellus'—through the development of a kind of pseudo-placental outgrowth from the maternal follicular epithelium which penetrates the embryo through a gap (wrongly called 'blastopore' by WILL) in the 'blastoderm' and ultimately fuses with the latter. By a disintegration of the pseudo-placental cells, there arises the 'secondary yolk' which comes to lie in the primary body cavity of the embryo and into which the already present yolk cells of the embryo wander. After a time the connection of the pseudo-placental 'secondary yolk' with the maternal follicular epithelium is severed.

- (ii) *Exclusively from the embryonic tissues.*—So far only the embryonic membranes have been known to form the pseudo-placenta. In *Archipsocus fernandi* (FERNANDO, 1934) it arises from the serosa in the posterior region (Text-fig. 10), and from both the amnion and



Text-fig. 10. Portion of sagittal section of posterior region of the embryo of *Archipsocus fernandi*, showing the connection of the serosa with the maternal ovarian tubule. (After FERNANDO, 1934.)

f., region of the fusion of serosa with wall of ovarian tubule; nut.m., nutritive mass; ov.t., wall of ovarian tubule; proct., wall of proctodæum; ser., serosa; th., thoracic leg.

the serosa in the anterior region. In both these regions the membranes fuse with the ovarian wall.

- (iii) *Both from the embryonic and the maternal tissues.*—In *Hemimerus talpoides* (HEYMONS, 1912) the pseudo-placenta is formed largely by the amnion, but in part probably by the maternal tissue also. This condition would, therefore, appear to occupy an intermediate

position between (i) and (ii) mentioned above, although it must be pointed out that the three kinds of pseudo-placentæ have been, in all probability, evolved quite independently of one another.

- (b) *Free embryo type*.—In this case the embryo lies freely in the maternal genital ducts and is not fixed in any way to the latter. The pseudo-placenta is formed, so far as is known, by the pleuropodia, as in *Hesperoctenes* (HAGAN, 1931) discussed above (p. 44). The pseudo-placenta has no direct connection with the maternal ovarian wall and only serves to absorb the nutritive fluids present in the oviduct. (Also see Appendix, p. 105.)

13. THE GENITAL CELLS.

The genital cells of insects are usually differentiated after the formation of the mesodermal somites and, indeed, from the latter. In numerous cases, however, they arise very early—sometimes during or even before cleavage—and then undergo a period of rest before acquiring their definitive position on the mesodermal somites and again becoming active. It is, therefore, desirable that we should be able to distinguish the exact point of time, in relation to other embryonic processes, when the genital cells arise. For this purpose, the following classification, where the insectan genital cells have been classified in accordance with the time of their appearance, has been proposed (ROONWAL, 1939, *b*). The classification is a modification of that originally proposed by SHINJI (1924).

1. *Pre-cleavage differentiation*.—Before cleavage begins. It is a kind of chemo-differentiation of the periplasm and, consequently, does not involve discrete cell or cell-like masses of protoplasm. It occurs in some Diptera, Coleoptera and probably the parasitic Hymenoptera.

2. *Cleavage differentiation*.—During cleavage. It occurs in some Diptera, such as *Chironomus* and *Miastor*.

3. *Post-cleavage differentiation*.—(Blastodermic differentiation of SHINJI.) After the end of cleavage but before the differentiation of the inner layer. It occurs in *Isotoma* (Collembola), *Forficula* (Dermaptera), *Vanessa* (Lepidoptera) and in some aphids and coccids.

4. *Differentiation from the inner layer*.—(Mesodermic differentiation of SHINJI.) Undoubtedly from the mesodermal elements of the inner layer. It occurs in most Pterygota.

14. THE BODY SCLERITES.

Embryology has recently thrown some light on the origin of two of the body sclerites, and these will be considered below.

(a) *The Basal Sclerites of the Labium.*

The difficulty of the homology of the basal sclerites of the labium has been discussed recently by SNODGRASS (1935), IMMS (1937) and others. Several writers have suggested, on morphological grounds, that while the mentum is of an appendicular origin and corresponds to the fused cardines of the first maxilla, the submentum is not truly appendicular but belongs to the sternal region of the labial segment.

Recent embryological evidence is entirely against this view. ROONWAL (1937) has shown that in *Locusta* no portion of either the labial or the prothoracic sternum takes part in the formation of the labial base, and the posterior border of the submentum represents the true anterior boundary of the prosternum. The labial sternum fuses with the two preceding sterna to form the hypopharynx. The mentum does not exist as a separate sclerite in *Locusta* but is probably fused with the submentum.

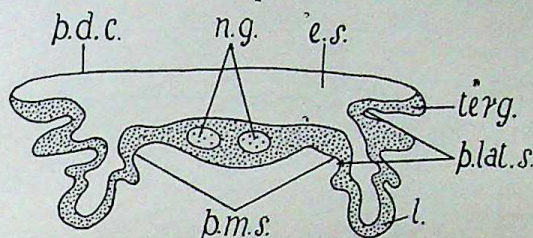
HOLMGREN (1909) maintained, also on embryological grounds, that the submentum of *Eutermes* is derived from the articulatory membrane between the labial and the first thoracic segments and, ontogenetically, is not a part of the labium. This view is at variance with the above-mentioned observations on *Locusta*. According to HEYMONS (1899), in Hemipteran embryos the various portions of the jaw appendages, such as the lacinia, galea, palpus, etc., arise independently and unite together secondarily to form the complete jaw appendage. No subsequent worker has confirmed this remarkable claim and it is difficult to accept it at present.

(b) *The Pleura* (Text-figs. 11 and 12).

HEYMONS (1899) first showed, on embryological evidence from the Hemiptera, that the insectan pleura in the thoracic region arise either wholly or in part from the subcoxa of their segments. Subsequently, several authors claimed this on purely morphological grounds (*vide* IMMS, 1937), and thus arose the 'subcoxal theory' of the origin of the pleuron. It is obvious that in deciding a problem of this nature, reference must be made to embryology, but for a long time HEYMONS's paper stood alone in this respect. Recently, however, ROONWAL (1937) has provided support for this theory from the condition obtaining in *Locusta* embryos, as will be evident from the following description taken from that author:—

The first division of each typical segment of the body (Text-fig. 11) is into a median sternum and two lateral *primary tergal sclerites*. The sternum is divisible into a median portion termed the *primary medio-sternite*, and two lateral portions, the

primary latero-sternites¹. The latter bear the appendages. The above description applies from the mandibular to the tenth abdominal segments, but what follows refers to the thoracic segments only. After blastokinesis the lateral edges of the embryo grow round and unite in the mid-dorsal line, thus forming a complete or *definitive tergum*. The articulations of the



Text-fig. 11. Diagrammatic representation of a transverse section across the metathorax of an embryo of *Locusta migratoria migratorioides* R. & F., shortly before blastokinesis, showing the primary tergal and sternal sclerites. (After ROONWAL, 1937.)

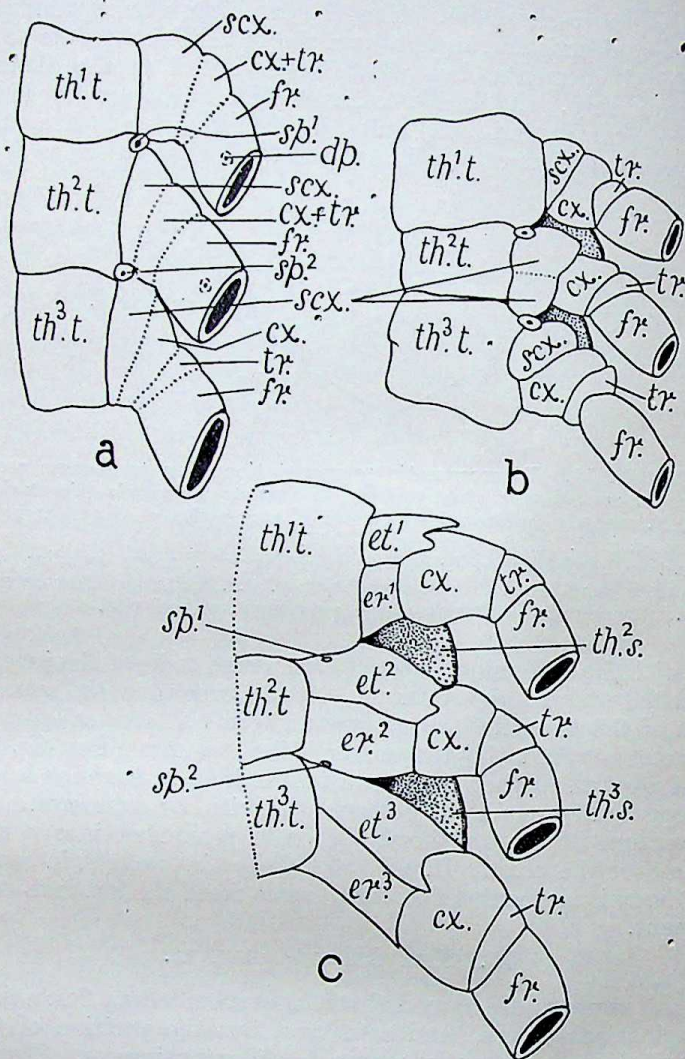
e.s., epineural sinus; l., metathoracic leg; n.g., nerve ganglia; p.d.c., first provisional dorsal closure of embryo; p.lat.s., primary latero-sternite; p.m.s., primary medio-sternite; terg., primary tergal sclerite.

legs with the body move laterally and come to lie at the junction of the tergum with the sternum. At the same time, the subcoxal joint of the thoracic legs grows and forms a large sclerite, the pleuron, between the tergum and the sternum (Text-fig. 12). Each pleuron further becomes divided into an anterior sclerite or episternum, and a posterior sclerite or epimeron. The episternum of the prothorax becomes prolonged into a short spine over the coxa. In this way the *entire* pleuron in each of the thoracic segments of *Locusta* arises from the subcoxa of its segment.

15. THE CORPORA ALLATA.

All workers are agreed that the corpora allata first arise as invaginations of the head ectoderm, but the position of these invaginations apparently varies in different insects. Thus, in *Forficula* (HEYMONS, 1895, a) they arise from the base of the first maxillæ; in *Apis* (NELSON, 1915) from the mandibular segment; in *Pieris* (EASTHAM, 1930, b) from the mandibular apodeme; and in *Carausius* (WIESMANN, 1926) and *Locusta* (ROONWAL, 1937) from the intersegmental membrane between the mandibular and the first maxillary segments.

¹ The term 'primary latero-sternites' is to be distinguished from the term 'latero-sternite' employed by the morphologists. Thus, SNODGRASS (1935) uses the latter term to denote the lateral portion of the definitive thoracic sternum 'apparently derived from the ventral arc (sternopleurite) of the subcoxa'.



Text-fig. 12 (a)-(c). Thoracic regions of embryos of *Locusta migratoria migratorioides*, R. & F. viewed from the side, showing the origin of pleura from the subcoxa. The legs are shown in part only. (a)—From embryo 120 hours old (at 33°C.). (b)—From embryo 7 days old, i.e., one day after blastokinesis. The mesothoracic subcoxa is seen dividing into an upper or episternal portion and a lower or epimeronic portion of the future pleuron. (c)—From a freshly hatched female hopper. (After ROONWAL, 1937.)

cx., coxa; dp., minute, evanescent femoral depressions of problematic significance; et¹-et³., episternum of 1st to 3rd thoracic segments; er¹-er³., epimeron of 1st to 3rd thoracic segments; fr., femur; scx., subcoxa; sp¹, sp²., first and second spiracles; th².s., th³.s., meso- and metathoracic sternum; th¹.t.-th³.t., 1st to 3rd thoracic terga; tr., trochanter.

However, in a recent work TIEGS and MURRAY (1938) have claimed that in the beetle *Calandra oryzae* the corpora allata are derived from the walls of the antennary coelom sacs. In other words, they are mesodermal in origin. Now, in several insects it has been clearly shown that while these organs first arise undoubtedly as ectodermal structures, they later become invested with a thin mesodermal coat from the inner walls of the antennary coelom sacs. In older stages it is difficult to distinguish this mesodermal covering from the ectodermal portion. TIEGS and MURRAY have probably failed to distinguish between the ectodermal origin of these organs and their secondary association with the antennary mesoderm, and it is difficult to accept their unique claim until adequate confirmation is forthcoming.

16. SOME EMBRYOLOGICAL PROBLEMS.

While a detailed study of the embryology of almost any insect is likely to yield new and valuable information, some important lacunae in our knowledge of this subject and certain special lines of fruitful investigation may be mentioned.

First of all, some of the primitive or otherwise interesting orders have not been worked out at all. These are: the Protura among the Apterygota; and the Mecoptera among the Pterygota. Among certain others, such as the Plecoptera, Isoptera, Embioptera, Psocoptera, Anopleura, Ephemeroptera, Thysanoptera, Neuroptera, Strepsiptera and the Aphaniptera, while some work has been done, further and fuller information is greatly needed. Thus, in the Strepsiptera, for example, HOFFMANN (1914) and NOSKIEWICZ and POLUSZYNSKI (1928) have obtained results of such great interest, especially with reference to early development and gastrulation, that one can confidently predict further important results in this group.

The early development of the parasitic Hymenoptera, especially the polyembryonic groups, and the precise origin of the embryonic envelopes in them, is a subject calling for enquiry.

The accumulation of embryological evidence in regard to head segmentation is another important subject of research interest in which has recently been rekindled by the discovery of labral and preantennary coelom sacs in *Carausius* and of the former alone in *Rhodinus* and *Locusta*.¹ It would consequently be of very great interest to investigate the cephalic coelom sacs and the development of the brain in the other Orthoptera as well as in other primitive insects.

The precise and detailed mode of differentiation, stage by stage, of the germ layers would provide extremely welcome information. It is essential that every event, however fleeting

¹ Also *Pteronarcys*, see Appendix, p. 105.

and apparently insignificant, in this process should be recorded as otherwise, we shall not be able to get beyond the stereotyped accounts of embolic and epibolic gastrulations which are only too well known. Before leaving early development, it may be pointed out that the kinetics of the cleavage cells, *i.e.*, their division and migration rates, the proportion of the primary yolk cells to other cleavage cells, and such other phenomena, have been so far investigated in very few insects, and more work is desirable in this field.

The rôle of the embryonic abdominal appendages in the formation of the uropods has been investigated in but few insects. The eighth and ninth abdominal appendages are generally believed to form the lower and upper ovipositor valves respectively of the female. These and other cognate phenomena must be investigated further before indisputable evidence can be said to have accumulated for the above view.

The origin of the mid-gut epithelium is too well known a problem to need emphasis and any new and exact information on that point cannot but be of interest. The claim of certain recent authors regarding the share which the yolk cells take in mid-gut formation is a point which especially needs confirmation. In this connection it may be mentioned that most authors have not been able to distinguish between primary and secondary yolk cells, although long ago GRABER (1891, *a*) had claimed that in *Melolontha* he could distinguish between the two kinds of yolk cells by their histological characters. This point deserves closer study. What happens to the primary yolk cells when the secondary ones begin to be formed? Do all of them degenerate; and do they become inextricably identified, in their morphology and their fate, with the secondary yolk cells? What is the life of a single yolk cell? Answers to these and other related questions are admittedly most difficult to obtain, but no serious attempts have been made in that direction. The recent work of TIRELLI (1926-1934) and other Italian workers has, however, opened up interesting possibilities in the field.

A critical study of the process of blastokinesis, as has recently been attempted in some grasshoppers and the silk-worm, is certain to yield valuable and interesting information if undertaken in other insects.

The origin of some of the body sclerites is a much-discussed problem largely because conclusions have hitherto been derived from theoretical evolutionary pictures based on morphology of the post-embryonic stages only. Embryological evidence, whenever available, has not failed to throw light on these discussions. Thus, the origin of the entire pleuron from the subcoxa and the truly appendicular nature of the labial submentum has recently been conclusively demonstrated in *Locusta*. But the development of these sclerites in other insects must be studied before generalizations of any value can be made.

I have indicated above only a few lines of research in descriptive or spatial embryology which are likely to prove fruitful. Rich subjects like bacterial symbiosis and experimental embryology are beyond the scope of the present work. In the former, BUCHNER and his school in Germany have produced extensive and extremely interesting work. In the latter, we have the pioneer works of HEGNER (1908-1911) in America; GEIGY (1931) in France, and, the most important of all, PAULI (1927), REITH (1925-1935) and of SEIDEL (1926-1936) and his school (KRAUSE, 1934, 1938; SCHNETTER, 1934, *a, b*; and MASCHLANKA, 1938) in Germany. In this connection, the helpful review of RICHARDS and MILLER (1937) also deserves mention. These fields, as well as that of embryonic physiology, lie almost virgin to-day and must be attacked.

IV. SUMMARY.

A brief historical sketch of the development of insect embryology, from the days of ARISTOTLE up to modern times, is given.

The carbolic-acid-and-water technique, evolved by SLIFER and KING (1933) has practically solved the difficulty of sectioning large yolky insect eggs.

The amplified theory of multi-phased gastrulation among insects (ROONWAL, 1939 *b*) is described. Its more important features are: (i) the suppression of the blastula stage; (ii) the spatial and temporal elongation of gastrulation and its consequent occurrence in several phases and sub-phases; (iii) the quadruple nature of all the three germ layers which are distinguishable firstly, into primary and secondly portions and secondly, into permanent and evanescent portions; and (iv) the tendency towards the suppression of the primary germ layers.

Some recent authors have shown that yolk cells definitely share in the formation of the mid-gut epithelium of certain insects.

HENSON'S (1932) unique claim of the endodermal origin of the insectan Malpighian tubules has been regarded by most authors as being devoid of foundation, and these structures are believed to be undoubtedly ectodermal.

A curious inversion of cell polarity has been recorded in the early embryos of some Strepsiptera.

Recent embryological evidence tends towards the establishment of two segments—the labral and the preantennary—lying in front of the antennary one, and thus towards the establishment of the 7-segmental nature of the insect head. The demonstration of the labral and the preantennary pair of coelom sacs in *Carausius* by WIESMANN (1926), and of the former alone in *Rhodinus* by MELLANBY (1936) and in *Locusta* by ROONWAL.

(1937)¹, provides support for this theory. A new interpretation of the composition of the insectan protocerebrum is presented according to which it is composed of two neuromeres which are assigned to the labral and the preantennary segments.

The pleuropodia of the viviparous Hemipteran, *Hesperoctenes fumarius* form, according to HAGAN (1931), a pseudo-placental organ. SLIFER (1937 and 1938, b) claims that in the grass-hopper, *Melanoplus*, the pleuropodia secrete an enzyme which aids in hatching. A new classification of insect pleuropodia into 'evaginate' and 'invaginate' types, based on their development, has recently been proposed.

FRIEDMANN (1934) has shown that the prolegs of the Lepidopteran caterpillars are direct derivatives of the embryonic abdominal appendages and must, therefore, be regarded as true segmental appendages.

Certain embryonic blood sinuses of considerable phylogenetic significance have been recorded in several insects. Their theoretical evolution in relation to the heart or mid-dorsal vessel of insects has been recently envisaged, and is described.

Three embryonic dorsal closures—two provisional and the third definitive—have recently been shown to occur in the Acrididæ. Their relation with the provisional and definitive mid-gut epithelia is intimate.

The precise mechanism of blastokinesis has been recently studied in great detail in certain insects and it has been established that the embryo undergoes blastokinesis by means of active movements of its own body. TIRELLI (1931, a) has suggested a spatio-mechanical theory of the origin of blastokinesis. According to it, insect blastokinesis originated owing to the need of the embryo for more space for its developing side.

HAGAN'S (1931) classification of the various types of viviparity among insects is described. A further sub-division of the type 'pseudoplacento-viviparity' is proposed.

A classification of the insectan genital cells, based on the time of their first appearance in the embryo, has recently been suggested.

It has been recently demonstrated that in *Locusta* no portion of either the labial or the prothoracic sternum takes part in the formation of the labial base and the posterior border of the submentum represents the true anterior boundary of the prosternum.

Recent embryological evidence strongly supports the theory of the origin of the thoracic pleura from the subcoxa.

The claim of TIEGS and MURRAY (1938) that the corpora allata in *Calandra* arise from the antennary mesoderm, instead of from the head ectoderm as in all other insects, does not appear to be well founded and cannot be accepted without further confirmation.

¹ Also in *Pteronarcys* by MILLER (1939), see Appendix, p. 105.

Some embryological problems, which call for enquiry and whose study is likely to yield fruitful results, are briefly described.

A complete and classified bibliography of insect embryology is appended.

V. BIBLIOGRAPHY.

An attempt is made here to compile as complete a list as possible of the literature on insect embryology up to the end of the year 1937. Papers appearing during 1938 and the early part of 1939 have also been included, but this period cannot be said to be complete. Notwithstanding my best efforts, a few references might still have been overlooked, and I shall be grateful to readers if they will kindly send me information about these. The majority of the references have been examined mostly in the Balfour and University Libraries, Cambridge; in the libraries of the Kaiser Wilhelm-Institut für Biologie and the Deutsches Entomologisches Institut, Berlin-Dahlem; in the Stattsbibliothek, Berlin; and in the library of the Zoological Survey of India, Calcutta. Those that could not be so examined have been taken from other sources, and I take this opportunity of expressing my gratitude to the numerous friends and workers who have helped me either by sending reprints of their works or in other ways.

To enhance its usefulness, this section is divided into two sub-sections as follows:—

1. *Alphabetical List.*—In this the author's name, the full title, etc., of the paper, and the journal in which it has appeared are given.

2. *Classified List.*—In this only the author's name and year, as appearing in the alphabetical list, are given. This sub-section is further divided as follows:

(a) *Classified according to insect orders.*

(b) *General.*—Under this are included those references which could not be easily classified under (a) above because they deal either with several insect orders, or with insects as a whole.

(c) *Experimental embryology.*—Under this are included those references which, while dealing mainly with the experimental side, also give observations on general embryology. They are also included under (a) above. It may be added that only the more important works have been included, and the list is by no means complete.

(d) *Bacterial symbiosis.*—Under this are included those references which, while dealing mainly with bacterial symbiosis in insect eggs, also give valuable

observations on insect embryology. They are also included under (a) above.

- (e) *Other Arthropods, etc.*—Under this are included a few references which, while dealing mainly with the embryology of Arthropods other than insects, deal, in addition, either with certain aspects of insect embryology, or are invaluable for the proper understanding of the latter from the comparative point of view.

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- 1883.—Materials for the study of the embryological development of *Geophilus ferrugineus* L.K. and *Geophilus proximus* L.K. (In Russian).—*Izviest. Imp. Obszczestw. Ljubytel. Estestowzn. Antrop.*, Moscow, vol. LIII.
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1938]

RECENT ADVANCES IN INSECT EMBRYOLOGY.

99

2. CLASSIFIED LIST.

(a) *Classified according to Insect Orders.*

(A)—APTERYGOTA.

1. Thysanura.

Grassi, B. (1884, *b*); Heymons, R. (1897, *a, b*); Heymons, R. and Heymons, H. (1905); Uzel, H. (1897, *a, b*); Silvestri, F. (1932).

2. Protura.

No references.

3. Collembola.

Barrois, L. (1879); Carl, F. (1903); Claypole, M.A. (1892; 1898); Folsom, H. (1900); Hoffmann, R. W. (1911); Lemoine, V. (1883); Oulganine, M. [Uljanin, M.] (1875; 1876); Packard, A. S. (1870; 1871, *a*); Philpitschenko, J. (1912, *a, b*); Prowazek, J. (1900); Ryder, J. A. (1886, *b*); Uzel, H. (1898).

(B)—PTERYGOTA.

(α) EXOPTERYGOTA.

4. Orthoptera.

Ayers, H. (1884); Baden, V. (1936); Baehr, W. B. Von (1907); Blochmann, F. (1887, *b*); Cappe de Baillon, P. (1920; 1925); Cappe de Baillon, P. and Pillault, R. (1937); Chodkowsky, N. A. (1888; 1890, *a, b*; 1891, *a, c, d*); Else, F. L. (1934); Faussek, V. (1911); Giardina, A. (1897); Graber, V. (1888, *a, c*; 1890; 1891, *a, b, e*); Hagan, H. R. (1917); Hallez, P. (1885; 1886); Hammerschmidt, J. (1910); Heymons, R. (1890; 1891, *a, b*; 1892; 1895, *a*; 1897, *c*); King, R. L. and Slifer, E. H. (1934); Korotneff, A. (1883; 1885); Krause, G. (1934; 1938); Lehmann, F. (1925); Leuzinger, H. and Wiesmann, R. (1925); McNabb, J. W. (1928); Nelsen, O. E. (1931; 1934, *a, b*); Nusbaum, J. (1883; 1886); Nusbaum, J. and Fulinski, B. (1906; 1909); Oka, H. (1934); Packard, A. S. 1883; Patten, W. (1884); Payne, N. M. (1934); Pflugfelder, O. (1937, *b*); Rabito, L. (1898); Rathke, H. (1832; 1844); Riley, W. A. (1904); Roonwal, M. L. (1935, *a, b*; 1936, *a, b*; 1937); Slifer, E. H. (1931; 1932, *a, b*; 1934; 1935; 1937; 1938, *a, b*); Slifer, E. H. and King, R. L. (1933; 1934); Strindberg, H. (1914, *b*); Stuart, R. R. (1935); Thomas, A. J. (1936); Thompson, V. (1934); Viallanes, H. (1890; 1891); Wheeler, W. M. (1889, *a*; 1890, *a, c, d*; 1893); Wiesmann, R. (1926).

5. Dermaptera.

Hansen, H. J. (1894); Heymons, R. (1893, *a*; 1895, *a*; 1909; 1912); Strindberg, H. (1915, *c*).

6. Plecoptera.

Miller, A. (1939).

7. Isoptera.

Holmgren, N. (1909); Knowler, H. M. (1896; 1900); Strindberg, H. (1913, *b*).

8. Embioptera.

Kershaw, W. (1914).

9. Psocoptera.

Fernando, W. (1934); Jentsch, S. (1936); Melnikow, N. (1869).

10. Anoplura (including Mallophaga).

Fernando, W. (1933); Grimm, O. (1870, *a*); Melnikow, N. (1869); Ries, E. (1931); Schlözel, G. (1937); Strindberg, H. (1916, *b*); Swammerdam, J. (1737); Weber, H. (1939).

11. Ephemeroptera.

Heymons, R. (1896, *a*, *c*); Joly, N. (1876, *a*, *b*).

12. Odonata.

Brandt, A. (1869); Graber, V. (1888, *a*); Heymons, R. (1896, *a*); Packard, A. S. (1868; 1871, *a*); Seidel, F. (1926; 1928; 1929, *a*, *b*; 1931; 1932; 1936); Tschuproff, Mme. H. (1903).

13. Thysanoptera.

Reyne, A. (1927).

14. Hemiptera.

Baker, A. C. (1921); Balbiani, E. G. (1866; 1871, *a*, *b*; 1885); Brandt, A. (1869); Brass, A. (1883); Breest, F. (1914); Buchner, P. (1911; 1918); Canto, P. (1896); Fijalkowska, J. (1928); Gillardi, H. (1934); Graber, V. (1878; 1888, *a*); Hagan, H. R. (1931); Henking, H. (1891, *a*); Herold, M. (1876); Heymons, R. (1899, *a*); Hirschler, J. (1911; 1912); Hussey, P. B. (1926); Huxley, T. H. (1858); Johnson, C. G. (1937);

Karawajew, W. (1893); Klevenhusen, F. (1927); Kozłowski, A. (1939); Leydig, F. (1848; 1850); Mellanby, H. (1935; 1936); Metschnikoff, E. (1866, *a, b*); Morgan, T. H. (1906); Morril, C. V. (1910); Muir, F. A. G. and Kershaw, I. C. (1911; 1912); Paillot, A. (1938); Pedaschenko, D. (1890); Pflugfelder, O. (1937, *a*); Phillips, W. J. (1915); Pierentoni, U. (1909; 1910, *a, b*; 1911, *a, b*; 1912, *a, b*; 1914, *a, b*); Poluszynski, G. (1911); Rondelli, M. (1925, *a, b*); Schrader, F. (1923); Seidel, F. (1924); Sell, W. (1919); Shinji, G. O. (1919; 1922; 1924); Speyer, W. (1929); Strindberg, H. (1919, *a*); Tannreuther, G. W. (1907); Teodoro, G. (1920); Tóth, L. (1933; 1935, *a, b*; 1937); Uichanko, L. B. (1924); Walczuch, A. (1932); Webster, F. M. and Phillips, W. J. (1912); Wheeler, W. M. (1889, *b, c*; 1890, *e*); Will, L. (1883; 1888, *a, b*); Witlaczil, E. (1884); Zacharis, O. (1884).

(β) ENDOPTERYGOTA.

15. Neuroptera.

Du Bois, A. M. (1936; 1938); Packard, A. J. (1871, *b*; 1872); Strindberg, H. (1915, *d*); Tichomirowa, O. O. (1890, *a, b*; 1892).

16. Mecoptera.

No references.

17. Trichoptera.

Graber, V. (1888, *a*); Marshall, W. S. (1907, *x*); Melnikow, N. (1869); Patten, W. (1884); Zaddach, G. (1854).

18. Lepidoptera.

Acqua, C. (1932, *a, b*); Bataillon, E. and Tehou-Su. (1928; 1931; 1933); Beer, S. (1932); Bobretzky, N. (1878, *a, b*); Christensen, P. J. H. (1937); Della Pieta, S. (1935); Drummond, M. (1936); Eastham, L. E. S. (1927; 1930, *b*); Foa, A. (1919, *a, b*); Friedmann, N. (1934); Ganin, M. (1869, *a*); Graber, V. (1888, *a*; 1890; 1891, *a*); Grandori, R. (1913; 1915, *a, b*; 1916; 1919, *a, b*; 1920; 1924, *a, b*; 1925, *a, b*; 1929, *a, b, c*; 1930; 1932, *a, b*); Hatschek, B. (1877); Henking, H. (1890); Henson, H. (1932); Hirschler, J. (1906; 1907, *a, b*); Huie, L. H. (1918); Ishiwata, S. (1913); Johannsen, O. A. (1929); Kowalewsky, A. (1871); Lautenschlager, F. (1932); Malpighi, M. (1669); Mariani, G. (1937); Maschlanka, H. (1938); Müller, K. (1938); Niceta, F. (1930); Nusbaum, J. (1884); Paillot, A. (1938); Planter, G. (1888); Rizzi, M. (1912); Saito, S. (1934; 1937); Schwangart, F. (1904; 1905; 1906); Schwartz, F. (1899); Sehl, A. (1931); Seiler, J. (1924); Selvatico, D. S. (1877; 1881; 1882); Strindberg, H. (1915, *b*); Suckow, F. W. L. (1818); Tichomiroff, A. (1879);

1882; 1887; 1891); Tirelli, M. (1926; 1928; 1929; 1930; 1931, *a, b*; 1934, *a, b*; 1935); Tonon, A. (1925; 1927, *a, b*); Toyama, K. (1902); Tutt, J. W. (1894); Ūmeya, Y. (1937); Vaney, C. and Conte, A. (1909; 1910); Verson, E. (1890; 1898; 1909); Wiesmann, R. (1935); Wong, W.-S. and Li, H.-H. (1934); Woodworth, C. W. (1889).

19. Coleoptera.

Blunck, H. (1914); (2) Brauer, A. (1925, *a, b*); Brauer, A. and Taylor, A. C. (1936); Bushnell, R. J. (1936); Butt, F. M. (1936); Carrière, J. (1891); Cody, F. P. and Gray, I. E. (1938); Czerski, S. (1904); Deegener, P. (1900); Emden, F. Van. (1925); Ewest, A. (1937); Friederichs, K. (1906); Fulinski, B. (1910; 1911); Graber, V. (1888, *a, b*; 1890, *a, b*; 1891, *a, b, d, e*); Hallez, P. (1886); Hegner, R. W. (1908; 1909, *a, b*; 1910; 1911, *a, b, c*); Heider, K. (1885; 1889; 1890); Hess, W. N. (1921); Hirschler, J. (1907, *c*; 1908; 1909, *a, b*); Hodson, A. C. (1934); Inkmann, F. (1933); Joly, M. (1844); Koch, A. (1931, *a, b*; 1936, *a, b*); Kölliker, A. (1842); Korschelt, E. (1912; 1924); Kowalewsky, A. (1871); Lécaillon, A. (1897, *a, b*; 1898, *a, b*); Longchamps, M. de S. (1904); Mansour K. (1927; 1934; 1936; 1938); Megusar, F. (1906); Melnikow, N. (1869); Metschnikoff, E. (1866, *b*); Nusbaum, J. (1889, *a, b*; 1890, *b*); Packard, A. S. (1872); Paterson, N. F. (1931; 1932; 1935); Patten, W. (1888); Petrunkewitsch, A. (1898); Pierantoni, U. (1927; 1929; 1930); Provasoli, L. (1932); Reith, F. (1935); Saling, T. (1907); Scheinert, W. (1933); Smreczynski, S. (1931; 1932; 1934); Tichomiroff, A. (1890, *a, b*); Tiegs, O. W. and Murray, F. V. (1938); Voeltzkow, A. (1889, *b*); Vogel, R. (1913); Wheeler, W. M. (1889, *a*); Wiemann, H. L. (1910, *a*; 1911); Williams, F. X. (1916); Wray, D. L. (1937).

20. Strepsiptera.

Brues, C. T. (1903); Hoffmann, R. W. (1913; 1914); Noskiewicz, N. and Poluszynski, G. (1924; 1928; 1935).

21. Hymenoptera.

Ayers, H. (1884); Bledowski, R. and Krainska, M. K. (1926); Blochmann, F. (1884; 1886; 1889); Bütschli, O. (1870); Butt, F. M. (1934, *a*); Carrière, J. (1890, *a, b*); Carrière, J. and Bürger, O. (1897); Daniel, D. M. (1932); Dickel, O. (1902; 1904); Doncaster, L. (1905); Ganin, M. (1869, *a*); Gatenby, J. B. (1917; 1918, *a, b*; 1920); Giard, A. (1898); Graber, V. (1888, *a*; 1890); Grandori, R. (1911); Grassi, B. (1884, *a*; 1886); Hecht, O. (1924); Hegner, R. W. (1914, *c*; 1915); Henneguy, L. F. (1891; 1892);

- Hill, C. C. (1922; 1923; 1926); Howard, L. O. (1937); Jackson, D. J. (1928; 1935); Kowalewsky, A. (1871); Kulagnin, M. N. (1890, *a, b*; 1892, *a, b*; 1897); Leiby, R. W. (1922; 1926; 1928); Leiby, R. W. and Hill, C. C. (1923; 1924); Kowalewsky, A. (1871); Lilienstern, M. (1933); Marchal, P. (1897, *a, b*; 1898, *a, b, c*; 1899; 1903; 1904, *a, b, c*; 1906; 1912); Marshall, W. S. (1907, *a*); Marshall, W. S. and Dernehl, P. H. (1905); Martin, F. (1914); Metschnikoff, E. (1866, *b*); Nelson, J. A. (1911; 1912; 1914; 1915; 1918); Packard, A. S. (1872); Paillot, A. (1937); Parker, H. L. (1931); Patten, W. (1887); Patterson, J. T. (1919; 1921); Petrunkevitch, A. (1901; 1902); Provasoli, L. (1932); Reith, F. (1931, *a*; 1932); Schleip, W. (1908); Schnetters, M. (1934, *a, b*); Silvestri, F. (1906; 1908, *a, b, c, d*; 1910; 1914; 1915; 1916; 1921); Speicher, B. R. (1936); Strindberg, H. (1913, *a*; 1914, *a*; 1915, *a, e*; 1916, *a*; 1917, *b*; 1919, *b*); Tanquary, M. C. (1913); Weismann, A. (1882).

22. Diptera.

- Auten, M. (1934); Baer, K. E. Von. (1863; 1866); Balbiani, E. G. (1885); Blochmann, F. (1887, *b*); Brauer, F. (1854); Bütschli, O. (1888); Butt, F. M. (1934, *a, b*); Child, G. P. and Howland, R. B. (1933); Craven, W. N. (1909); Du Bois, A. M. (1932; 1933, *a, b*); Escherich, K. (1900, *a, b*; 1902, *b*); Felt, E. P. (1911, *a, b*); Gabritschewsky, E. (1928); Gambrell, F. L. (1933); Geigy, R. (1931); Graber, V. (1888, *a*; 1889, *b*; 1891, *a*); Grimm, O. (1870, *b*); Hasper, M. (1911); Hegner, R. W. (1912); Henking, H. (1888, *b*); Hinman, E. H. (1932); Holmgren, N. (1904); Howland, R. B. and Child, G. P. (1933; 1935); Howland, R. B. and Sonnenblick, B. P. (1936); Huettner, A. F. (1923; 1935); Jaworowski, A. (1879; 1882); Kahle, W. (1908); Kölliker, A. (1842); Kowalewsky, A. (1886); Kupffer, C. (1866; 1867); Lassmann, G. W. P. (1936); Leuckart, R. (1858; 1865); Lowne, B. (1895); Melnikow, N. (1869); Metschnikoff, E. (1865; 1866, *b*); Miall, L. C. and Hammond, A. R. (1900); Noack, W. (1901); Parks, H. B. (1935; 1936); Pauli, M. E. (1927); Poulsen, D. F. (1937, *a, b*); Pratt, H. S. (1900); Rabinowitz, M. (1937); Reith, F. (1925); Ritter, R. (1890); Sachtleben, H. (1918); Schaefer, P. E. (1938); Schmidt, F. (1889); Schmuck, M. L. and Metz, C. W. (1932); Strasburger, E. H. (1934; 1935); Strasburger, E. H. and Körner, L. (1939); Voeltzkow, A. (1888; 1889, *a*); Weismann, A. (1863; 1864, *b*; 1882); Wheeler, W. M. (1891, *a*).

23. Aphaniptera.

- Balbiani, E. G. (1875); Leeuwenhoek, A. Van. (1695); Packard, A. S. (1872); Strindberg, H. (1917, *a*); Weismann, A. (1863).

(h) *General.*

Agásiz, L. (1851); Baer, K. E. Von. (1828); Balbiani, E. G. (1882; 1885); Balfour, F. M. (1880); Berlese, A. (1898; 1899; 1909; 1913); Blochmann, F. (1887, *b*, *c*); Bobretzky, N. (1878); Brandt, A. (1876; 1880, *a*, *b*); Braem, F. (1895); Bruce, A. T. (1887); Buchner, P. (1930); Bugnion, E. (1921); Burmeister, H. (1836); Carrière, J. (1891); Cholodkowsky, N. (1889; 1891, *b*, *c*); Dawydoff, C. (1928); Deegener, P. (1914); Depdolla, P. (1928); Dohrn, A. (1866; 1876); Eastham, L.E.S. (1930, *a*); Emery, (1889); Escherich, K. (1900, *c*; 1901; 1902, *a*); Faussek, V. (1911); Gadzikiewicz, W. (1905); Ganin, M. (1869, *b*; 1874, *a*, *b*); Goodrich, E. S. (1895; 1897); Graber, V. (1877-1879; 1878; 1879; 1888, *a*, *b*, *c*; 1889, *a*, *b*, *c*; 1890, *a*; 1891, *a*, *b*, *c*, *e*, *f*); Grassi, B. (1889); Haase, E. (1889, *a*, *b*); Haeckel, E. (1874; 1877); Hallez, P. (1886; 1887); Hegner, R. W. (1911, *c*; 1914, *a*, *b*; 1917); Heider, K. (1897; 1928); Henking, H. (1888, *a*; 1891, *b*; 1892); Henneguy, L. F. (1904); Henrikson, K. (1928); Hertwig, O. (1906); Hertwig, O. and Hertwig R. (1881); Hertwig, R. (1881); Heymons, R. (1893, *b*; 1894, *a*, *b*; 1895, *b*; 1896 *b*, *d*; 1897, *d*, *f*; 1898, *b*; 1899, *b*; 1905); Heys, F. (1931); Hirschler, J. (1924; 1939); Hussey P. B. (1926); Imms, A. D. (1934; 1937); Jackson, D. J. (1935); Jaworowski, A. (1882; 1891; 1897); Joly, N. (1844); Kellog, V. L. (1902); Kessler, Fr. H. (1879); Kölliker, A. (1842); Korotneff, A. (1894); Korschelt, E. (1936); Korschelt, E. and Heider, K. (1892; 1910); Kowalewsky, A. (1871); Lang, A. (1891; 1903); Leeuwenhoek, A. Van. (1695); Leiby, R. W. (1928); Lubbock, J. (1859); Macbride, E. W. (1914); Mayer, P. (1876); Melnikow, N. (1869); Metschnikoff, E. (1866, *b*); Needham, J. (1931; 1934); Nusbaum, J. (1889, *b*; 1890, *a*); Packard, A. S. (1872; 1875); Pander, H. C. (1817); Patten, W. (1887; 1890); Patterson, J. T. (1927); Petrunkevitch, A. (1933); Rabl, C. (1889); Redi, F. (1688); Richards, A. G. (1932); Robin, C. (1862, *a*, *b*); Roonwal, M. L. (1939, *a*, *b*); Ryder, J. A. (1886, *a*); Sammogia, A. (1932); Schinkewitsch, W. (1885); Schneider, A. (1883, *a*, *b*; 1885, *a*, *b*); Silvestri, F. (1937); Smith, J. B. (1896); Snodgrass, R. E. (1925; 1928; 1935; 1938); Swammerdam, J. (1737); Tichomiroff, A. (1892); Wagner, J. (1894); Weber, H. (1937, *a*, *b*; 1938); Weismann, A. (1864, *a*; 1882); Wheeler, W. M. (1890, *b*; 1891, *b*, *c*; 1892, *a*, *b*); Wielowiejski, H. R. (1886); Willey, A. (1899); Wolff, C. F. (1759); Zaddach, G. (1867); Zograf, N. [Sograff, N.] (1892).

(c) *Experimental Embryology.*

Geigy, R. (1931); Hegner, R. W. (1908; 1909, *a*, *b*; 1910; 1911, *a*, *b*, *c*); Howland, R. B. and Child, G. P. (1935); Howland, R. B. and Sonnenblick, B. P. (1936); Huxley, J. S. and De Beer,

G. R. (1934); Krause, G. (1934); Maschlanka, H. (1935); Megusar, F. (1906); Morgan, T. H. (1927); Oka, H. (1934); Pauli, M. E. (1927); Reith, F. (1925, 1931, *a, b, c*; 1932; 1935); Richards, A. G. and Miller, A. (1937); Schnetter, M. (1934, *a, b*); Seidel, F. (1926; 1928; 1929, *a, b*; 1931; 1932; 1934; 1935; 1936); Thompson, V. (1934).

(d) *Bacterial Symbiosis.*

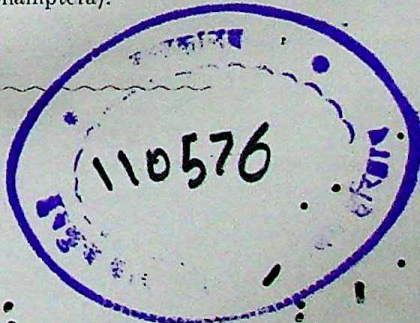
Blochmann, F. (1887, *a*; 1892); Breest, F. (1914); Grandori, R. (1924, *a*; 1929, *a*); Hecht, O. (1924); Hinman, E. H. (1932); Klevenhusen, F. (1927); Koch, A. (1931, *a, b*; 1936, *a, b*); Lilienstern, M. (1933); Peirentoni, U. (1909; 1910, *a, b*; 1911, *a, b*; 1912, *a*; 1914, *c*; 1920; 1923; 1924; 1927; 1929; 1930); Ries, E. (1931); Rondelli, M. (1925, *a, b*); Scheinert, W. (1933); Tóth, L. (1937); Walczuch, A. (1932).

(e) *Other Arthropods, etc.*

(1) Brauer, A. (1894; 1895); Cholodkowsky, N. (1895); Faussek, V. (1911); Glen, E. H. (1919); Goodrich, E. S. (1895; 1897); Grassi, B. (1884, *b*); Heymons, R. (1897, *e*; 1898, *a*; 1901); Kennel, J. (1885; 1888); Kishinouye, K. (1894); Manton, S. M. (1928; 1934); Metschnikoff, E. (1874; 1875); Nair, B. (1939); Pflugfelder, O. (1932); Roonwal, M. L. (1939, *a*); Slater, W. L. (1888); Sedgwick, A. (1885; 1886; 1887; 1888); Sheldon, L. (1889); Silvestri, F. (1932); Sollaud, E. (1933); Suckow, F. W. L. (1818); Tiegs, O. W. (1939); Willey, A. (1898); Zograf, N. [Sograff, N.] (1882; 1883).

VI. APPENDIX.

While this work was in the press, three noteworthy papers have appeared which deserve mention. Firstly, H. R. HAGAN (*Ann. Entom. Soc. Amer.*, vol. XXXII, pp. 264-266, 1939) describes in a viviparous cockroach of the Hawaiian Islands, *Diploptera dytiscoides*, remarkably long and tubular pleuropodia which presumably convey nutriment from the maternal genital cavity to the embryo through the micropylar aperture in the egg-wall. Secondly, in an advance abstract of his dissertation on the embryology of *Pteronarcys prateus* (Plecoptera), kindly sent by Dr. A. MILLER (for Part I, already published, see p. 83), it is shown that the *labral*, antennary, intercalary, mandibular, maxillary and labial pairs of coelom sacs are developed in the head, the *labral* pair being of special interest. Lastly, E. L. KESSEL (*Smithsonian Misc. Coll.*, vol. XCVIII, No. 3, 1939) gives us the first comprehensive account of the embryology of some fleas (Aphaniptera).



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CALCUTTA:—Published by the Royal Asiatic Society of Bengal, and Printed
by P. Knight, Baptist Mission Press, 41A, Lower Circular Road.

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